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IN MEMORIAM: FRANCES HAMERSTROM

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Frances Hamerstrom died 29 August 1998 at age 90 in Port Edwards, Wisconsin, U.S.A. Fran (pronounced Fron) was well known for her work on Greater Prairie Chickens (*Tympanuchus cupido*), Sharp-tailed Grouse (*Pedioecetes phasianellus*) and Northern Harriers (*Circus cyaneus*). She published over 150 scientific papers, dozens of popular articles and 12 books. She once remarked that "if you are the kind of person who wakes up every morning wanting to make the world a better place, it gives a certain zest to everything you do." Those who knew Fran will agree; there was a certain zest to everything she did.

Despite the societal stuffiness of her privileged childhood, Fran was drawn to wild animals at an early age. Her fondness for raising young wild animals and nursing sick ones to health reinforced in her mind that she was different from other people in her social setting. It also laid the foundation for a "hands-on" style of wildlife research that emphasized personal contact with the animals of study. To Fran, bringing free-flying raptors into her household to study them just made good sense. It seemed odd to her to think that a scientist could ask meaningful research questions without having first-hand knowledge of an animal's daily needs.

Fran's research style and personality complimented those of her husband and teammate, Frederick (known to his friends as Hammy), who preceded her in death by eight years. This exceptional life-long team was appropriately labeled a "super organism" by an anonymous apprentice. Thus, it is virtually impossible to refer to them individually in their wildlife careers. That is not to say that they behaved alike. Fran was often spontaneous and impulsive whereas Frederick was methodical and meticulous. Fran was sometimes outspoken and prone to embellishment whereas Frederick was the quiet master of understatement. Both were fiercely committed to saving our natural heritage. They accomplished so many things together because their differences strengthened their sum.

Fran was in the vanguard of "equal opportunity" for women in wildlife biology long before it was popular or even considered. The male-oriented profession precluded specific employment in her early professional life and significantly limited it later on. Fran was keenly aware of the male chauvinism associated with the embryonic wildlife profession and would subtly call attention to this fallacy by physically out-manning men in the field. Her relatively recent book, "Is She Coming Too?" is testament to this historic awareness. When Frederick gained an educational appointment, or employment, Fran accompanied him and participated as a volunteer, or pursued complimentary avenues. Her efforts were soon recognized and occasionally rewarded with a token salary, but more often the agency got two highly qualified people for the price of one. Thus, the Hamerstroms jointly conducted field research on pheasant, Northern Bobwhite (*Colinus virginianus*), hawks and owls under Paul L. Errington at Iowa State College from 1932-35, and research on prairie chickens, Sharp-tailed and Ruffed (*Bonasa umbellus*) Grouse, Sandhill Cranes (*Grus canadensis*), furbearers, and Great Horned Owls (*Bubo virginianus*) for the U.S. Resettlement Administration in central Wisconsin from 1935-37. While at Iowa, Fran received an award for "the woman most likely to succeed in research". The Hamerstroms studied prairie chickens as Research Fellows under Aldo Leopold at the University of Wisconsin (1937-41), where Fran became the only woman to ever earn a graduate degree (M.S.) under Professor Leopold. They conducted joint research on deer, songbirds, small mammals, prairie chickens, and Sharp-tailed Grouse through the University of Michigan Museum of Zoology (1941-49) with a leave for military duty (1943-46) during which time, Fran was a medical technician in the laboratory of U.S. Army Beaumont General Hospital, El Paso, TX U.S.A. They became project leaders of the Wisconsin Department of Natural Resources Prairie Grouse Management Research Unit with headquarters in Plainfield, WI U.S.A. (1949-72). During this tenure, they gained international recognition for their scholarship and successful efforts to ensure a permanent place for prairie chickens on the Wisconsin landscape. Fran was awarded an honorary doctorate degree from Carroll College in Waukesha, WI U.S.A. in 1961. Upon retirement from the Wisconsin Department of Natural Resources in 1972, they became unsalaried Research Associates at the University of Wisconsin-Stevens Point and continued wildlife research until their respective deaths. Their lifetime achievements are even more remarkable when one considers that they conducted exhaustive field studies on harriers, Osprey (*Pandion haliaetus*), kestrels, Harris Hawks (*Parabuteo unicinctus*) and several other species coincident with their tenure on other official projects. They were stellar role models.

Although Fran's research on grouse was more noteworthy to many, she always held a special fascination with raptors. Her first major scientific paper (co-authored with Errington and Frederick) was on the food habits of Great Horned Owls. It won The Wildlife Society's Terrestrial Publication Award in 1940. Ironically, the paper was a disappointment to her. As a woman in a male-oriented profession, she felt a strong need to prove herself by publishing her first significant paper as the sole author. Errington just assumed she would want her relatively small contribution to become part of his major paper. She went on to publish 70 papers on birds of prey and to receive The Wildlife Society's publication award (as a co-author with Frederick and Os Mattson) a second time in 1957 for her work on prairie chicken management.

One of Fran's most exhaustive studies was a long-term project on the breeding ecology of Northern Harriers in central Wisconsin. From the 1950s to 1980s she and co-workers banded close to 300 adult and 650 nestling harriers, and conducted over 20,000 small mammal trap nights. She documented that food abundance was the mechanism regulating harrier mating systems and local population densities. She also noted that those relationships changed during the years that the pesticide DDT was used. Keeping with her habit of maintaining several research projects simultaneously, Fran also conducted a long-term nest box study of American Kestrels (*Falco sparverius*). During the winters of their later years, she and Frederick conducted studies on Harris Hawks in Texas and Ospreys in Mexico.

Raptors held more than a scientific interest for Fran. She was an accomplished falconer who, at age 12, took her first quarry with a male kestrel. Later she helped pioneer artificial insemination techniques with Golden Eagles (*Aquila chrysaetos*). It was not uncommon for Fran to apply traditional falconry techniques in her raptor research projects. She maintained close ties to falconers throughout her life and was a member of the North American Falconers Association, the British Falconers Association and the Great Lakes Falconers Association.

Her lifetime interest in raptors also made Fran an early supporter of the Raptor Research Foundation. She received the President's Award from the Foundation and was the Central Director in 1975–76. In 1990, the Foundation created an award in the Hamerstrom name given to individuals who made significant contributions to the understanding of raptor ecology or natural history. In 1992, the Journal of Raptor Research dedicated a special issue to the Hamerstroms' contribution to science. Upon Frederick's death, Fran journeyed to tropical rainforests, a region that apparently always intrigued her but which Frederick had little desire to visit because of the heat and humidity. She initially traveled to the Congo where she "hunted with the pygmies" as she put it. She made at least five consecutive trips to the Amazon basin, always traveling alone and training physically for the ordeal beforehand. She was initially interested in the hunting practices of rainforest societies and started to collaborate on a book on that subject with a native. But, like the birds she studied, Fran returned to Wisconsin each spring to continue her research on kestrels.

Few people in the profession of wildlife biology have earned so many awards from such a breadth of organizations. She received the Josselyn Van Tyne Award from the American Ornithologist's Union, the Chapman Award from the American Museum of Natural History, the United Peregrine Society Conservation Award and the Edwards Prize from the Wilson Ornithological Society. A sample of other organizations that bestowed awards include the Raptor Research Foundation, The Wildlife Society, National Wildlife Federation, International Crane Foundation, Citizens Natural Resources Association, Deutschen Ornithologen—Gesellschaft, Wisconsin Department of Natural Resources, Wisconsin Society for Ornithology and Wisconsin Academy of Sciences, Arts and Letters. Fran was a member of over 20 scientific societies including all the major North American and several European ornithological societies, The Wildlife Society, Raptor Research Foundation, Ecological Society of America and the American Society of Mammalogists. She also was a member of several wildlife conservation societies and writers associations. In the last 20 years of her life, Fran devoted more time to writing popular books and preferred to be defined as a writer rather than an international wildlife biologist. Her book "Strictly for the Chickens" won the August Derleth Award.

One of Fran's least-recognized contributions to the field of science was her service as an educator and role model. The Hamerstroms employed a European model of apprenticeship whereby they allowed qualified individuals to live in their home and become part of their daily lives. The 100 or so apprentices were called gabboons. The term means slaves that conduct the lowest form of labor. During the banquet at a Raptor Research Foundation annual meeting, Fran looked around the room and pointed out the large number of Foundation officers and meeting attendees who had been through the Hamerstrom household. It was a testament to the influence the Hamerstroms have had on the field of raptor research.

The gabboon system ensured that science was only part of an apprentice's learning experience. Gabboons were treated to introductions with visiting professionals from all over the world. Since before World War II, the Hamerstroms had strong connections to European scientists. Gabboons were schooled in subjects as diverse as proper table manners, correct English and carpentry. They also enjoyed Fran's fine cuisine, which was the subject of her wild foods cookbook. Anyone who washed dishes and put the antique china back in the cupboards quickly realized that every piece had its place and it was not negotiable. Certain strict household rules evolved as a defense mechanism against legions of houseguests each year. Like Leopold, the Hamerstroms imparted on gabboons a strong appreciation for fine art and disdain for the trappings of technology. The walls of their unpainted pre-civil war construction

farmhouse in rural central Wisconsin were adorned with original art work. The house had no indoor plumbing but each person was allowed private bathing time at “the pond” where they had a chance to see a Green Heron (*Butorides striatus*) or a brood of Wood Ducks (*Aix sponsa*).

Fran’s model for a biologist was one with more field sense than statistical prowess or experimental design skills. This view was also evident in most of her publications, which often lacked statistical rigor but were rich with high-quality data. Her thoughts on statistics were that if a pattern wasn’t obvious from a look at the raw data, it either wasn’t real or more samples were needed to know for sure. She lamented the fact that contemporary students often knew very little basic biology about the animals they were studying even though they may have had a good grasp on the scientific process.

The Hamerstroms set the standard for a dedicated work ethic. They used their home as a research center, they brought gabboons into their daily lives and they believed that if animals did not recognize weekends and eight-hr days, it didn’t make sense for researchers to do so either. It was obvious that wildlife research was more of a passion for the Hamerstroms than a job. This philosophy stemmed from Leopold’s expectations of his graduate students and was the basis for the “Hamerstrom rule of thirds”. The rule is that researchers should spend one-third of their time on the bureaucratic folly required by their employer, another one-third of their time should be spent on tasks both the employer and the researcher want to do and one-third of their time should be spent doing exactly what the researcher pleases. Fran was quick to note that this last one-third was beyond a regular 40-hr week, and she maintained it was that portion of their time that made the prairie chicken work a success. Even while in Michigan from 1943–46, she and Frederick took personal time to visit the booming grounds in central Wisconsin each year to monitor their marked birds.

Fran also was a model in her advocacy of keeping wild pets. She believed that if the public was to really appreciate wild animals they must be allowed to experience them first hand, much as she had done as a child. She believed the risk of harm to an individual wild pet was less than the benefit of letting a child feel the wonder and responsibility of caring for that pet. Although Fran rehabilitated many injured wild animals over her lifetime, she realized in mid life that emphasizing the welfare of an individual animal over that of the population was misguided. In her book *Strictly for the Chickens*, Fran tells the story of capturing a hen prairie chicken with a nasty infection. Frederick was ready to end the bird’s suffering and make a study skin from it. Fran intervened and cleansed the wound, stitched it up and released the bird. Years later she recaptured the same hen and thus became somewhat of a heroine for saving its life. Of that incident Fran wrote, “But year after year I watched the range of our prairie chickens disappear under the plow and drainage. And I began to grow up. I came to realize that the saving of one individual for sentimental reasons is nothing compared to preservation of habitat for a species. Frederick knew this all the time.”

Even in death Fran was a role model. She saw countless life and death cycles through harrier and vole population highs and lows. Better than most people she knew that in nature, death was necessary and healthy for the good of the population. As with her husband, Frederick, and former professor, Aldo Leopold, there was no funeral so that death would be mourned; funerals are for the living and the commercial enterprises that materialize out of the death event. Instead she slipped quietly away to become part of that natural cycle she spent her life preserving.

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INTRA- AND EXTRA-PAIR COPULATIONS AND FEMALE REFUSAL OF MATING IN MONTAGU'S HARRIERS

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ABSTRACT.—We studied the mating behavior of Montagu's Harriers (*Circus pygargus*) and recorded the incidence of extra-pair copulations (EPC) and refusal of females to copulate. The average duration of copulations was 4.9 sec and they were most frequent between 1000–1400 H. Each pair averaged 105 successful copulations per clutch (range = 31–245). About 59% of 114 within-pair copulation (WPC) attempts were unsuccessful and, in 14 cases, the female rejected its mate. For the majority of cases, the cause of copulation failure was not identified. While the frequency of copulation attempts was not correlated with food-pass frequency, the duration of copulations was influenced by the presence of food brought by the male. Copulation attempts peaked early in the breeding season (3 wk prior to the beginning of egg laying) and outside the fertile period of females. Successful copulations peaked early in the breeding season (wk 4) and during the females' fertile period (wk 1). Copulation early in the breeding season may function to assess male competence in Montagu's Harriers allowing a way for females to evaluate the quality of males. Refusal is an aspect of female behavior that could help us to understand if, and in what way, female choice is based on the capacity of the male to successfully transfer sperm.

KEY WORDS: *Circus pygargus; Montagu's Harrier; copulation; extra-pair copulation; copulation refusal.*

Intra- and extra-pair copulations y rechazo de la hembra de ser montada en el Aguilucho Cenizo

RESUMEN.—El motivo de este estudio es de presentar observacione de las montas del Montagu's Harriers (*Circus pygargus*) y de discutirlo en relación a extra-pair copulations (EPC) y el rechazo de la hembra de ser montada. La media de duración de la monta era 4.9 y las cópulas eran más frecuentes entre 1000–1400 H. Cada pareja lleva a cabo una media de 105 cópulas exitosas por puesta (rango = 31–245). Alrededor del 59% de 114 WPC intentos fueron fallidos y en 14 casos observamos que la hembra rechazaba su macho. Para la mayoría de los otros casos no identificabamos cual era la causa del fallo en la cópula. La frecuencia de los intentos en la copulación no está correlacionada con la frecuencia de trasferencia de alimentos, pero la duración de las copulaciones se ha encontrado que está influenciada por la presencia del alimento llevada por el macho que lleva a cabo la mayoría de los intentos cuando la probabilidad de éxito es mayor, y por tanto cuando la hembra ha recibido o está comiendo la presa. La variación estacional en los intentos de cópula muestran un pico temprano en la temporada de cría (tres semanas ante de la deposición de los huevos, o semana 3) y fuera del periodo fértil de la hembra. La frecuencia exitosa de cópulas muestran dos picos: uno temprano en el periodo reproductor (semana 4) y otro durante el periodo fértil de la hembra (semana 1). Por lo tanto, la cópula, especialmente aquellas durante las etapas tempranas del periodo reproductor, pueden tener una función social importante en el Montagu's Harrier. Para la hembra pudiera ser una forma de evaluar la calidad del macho y el rechazo es un aspecto del comportamiento de la hembra, que podría ayudarnos a entender si, y en que manera, la elección de la hembra está basada en la capacidad del macho para alcanzar cópulas exitosas.

[Traducción de Fernando Hiraldo]

The Montagu's Harrier (*Circus pygargus*) is generally monogamous (Cramp and Simmons 1980) but occasionally is polyandrous (Pandolfi et al. 1995, Arroyo 1996) or polygynous (Hens 1926 in Cramp and Simmons 1980, Dent 1939, Underhill-Day 1990). Its copulation behavior is relatively unknown. In monogamous species investing heavily in parental care, Trivers (1972) predicted that natural selection should favor males that pursue a mixed reproductive strategy. Therefore, males increase their fitness by mating with and fertilizing females that have already mated and whose young will be reared without their help. The benefits of extra-pair copulations (EPC) for females are not as clear, especially when females actively resist (McKinney et al. 1984). On the other hand, females apparently go in search of EPCs and data suggest that they sometimes solicit EPCs from males with higher quality than their partners (Birkhead and Møller 1992, Kempenaers et al. 1997). Numerous instances have been reported of females refusing to mate with their partners (Indigo Buntings [*Passerina cyanea*], Westneat 1987; Tree Swallows [*Tachycineta bicolor*], Venier and Robertson 1991; White Storks [*Ciconia ciconia*], Tortosa and Redondo 1992; Willow Warblers [*Phylloscopus trochilus*], Arvidsson 1992; Red-billed Gulls [*Larus novaehollandiae*], Mills 1994; Razorbills [*Alca torda*], Wagner 1996; Ospreys [*Pandion haliaetus*], Birkhead and Lessells 1988; African Marsh-Harriers [*Circus ranivorus*], Simmons 1990; Black Kites [*Milvus migrans*], Koga and Shiraishi 1994).

This study was undertaken to observe the mating behavior of Montagu's Harriers in reference to EPCs and refusals by females to copulate.

STUDY AREA AND METHODS

We observed the behavior of the Montagu's Harrier at two sites in the Pesaro-Urbino area (Monte della Matteringa: $43^{\circ}46'20''$, $12^{\circ}51'20''$ and Montefabbri: $43^{\circ}46'00''$, $12^{\circ}40'50''$), Marche region, Italy from 1991–96. Breeding sites were in the foothills of the Apennines (altitude 200–500 m) and consisted of uncultivated steep badlands and wheat crops.

Four to six pairs of Montagu's Harriers nested in loose colonies at the two sites. Individuals were identified by molt and plumage color and consistent use of perches. We were able to identify individual birds in six of the 24 pairs studied and only data derived from these six pairs are presented. We collected 512 hr of observations on these six pairs from the time they arrived at nesting sites until the time they left. Observations were made between sunrise and sunset for five consecutive hours of observation each day. This allowed us to cover all daylight hours over the period of one week with three shifts. Ob-

servations were made using 10×50 binoculars and a 30× spotting scope.

The term copulation attempt was used to refer to copulation attempts by males regardless of their success. We assumed that the time needed for the male to balance on the back of the female before cloacal contact was at least 3 sec; therefore all attempts lasting <4 sec were classified as unsuccessful (Simmons 1990). Copulation attempts were considered as individual cases even if they occurred during a succession of attempts by the male. Refusals to mate by females were only counted if we were certain that their behavior did not allow males to land on their backs, or if their behavior caused males to lose their balance and take flight within 1 sec.

In birds, the length of the female's fertile period depends on various factors: duration of sperm storage in the female reproductive tract, time interval between the fertilization of an egg and its subsequent deposition, and number of days in which the clutch is completed (Birkhead 1988, Birkhead and Møller 1992). The duration of sperm storage and the time interval between fertilization of an egg and its subsequent deposition have not yet been established in the Montagu's Harrier; therefore, in order to hypothesize the duration of the presumed female fertile period, we used data for the American Kestrel (*Falco sparverius*, Bird and Buckland 1976), where the duration of sperm storage in the female lasts about 8 d. We assumed that sperm storage in female Montagu's Harriers was about 6 d prior to egg laying, given that this is the shortest period of sperm storage known (Birkhead and Møller 1992). The time between ovulation and deposition of an egg is about 24 hr in domesticated fowl (Birkhead and Møller 1992). Fertilization takes place within one hour of ovulation, so we assume a period of one day between fertilization and egg deposition for the Montagu's Harrier. We assumed that the female fertile period began on the seventh day (6 + 1) before the deposition of the first egg and ended about one day before the deposition of the last egg. Egg laying was determined by observing nests with the aid of a mirror which allowed us to see the eggs while maintaining a distance of about 3 m from the nest. We counted back 29 d (Cramp and Simmons 1980) from the date of hatching in order to obtain the date on which egg laying occurred. The date of hatching was estimated by counting back from the age of the oldest chick which was estimated from morphological characters (Cramp and Simmons 1980). We assumed an average of 2 d between laying of each egg (Cramp and Simmons 1980, Glutz et al. 1971).

We divided the reproductive season into weeks, calling the week in which eggs were laid wk 0. The courtship period included wk -4, -3, -2; the presumed female fertile period was wk -1 and wk 0. We assumed that egg laying started on first day of wk 0.

We recorded behavior 5 min before and 5 min after copulation attempts. Because both males and females can show more than one display during this 5-min period, the proportion of each display type (expressed as a percentage) exceeded 100%. The various displays are defined in Pandolfi and Pino D'Astore (1990). With the term "sky-dance" we mean sky-dancing plus spiraling *sensu* Simmons (1991).

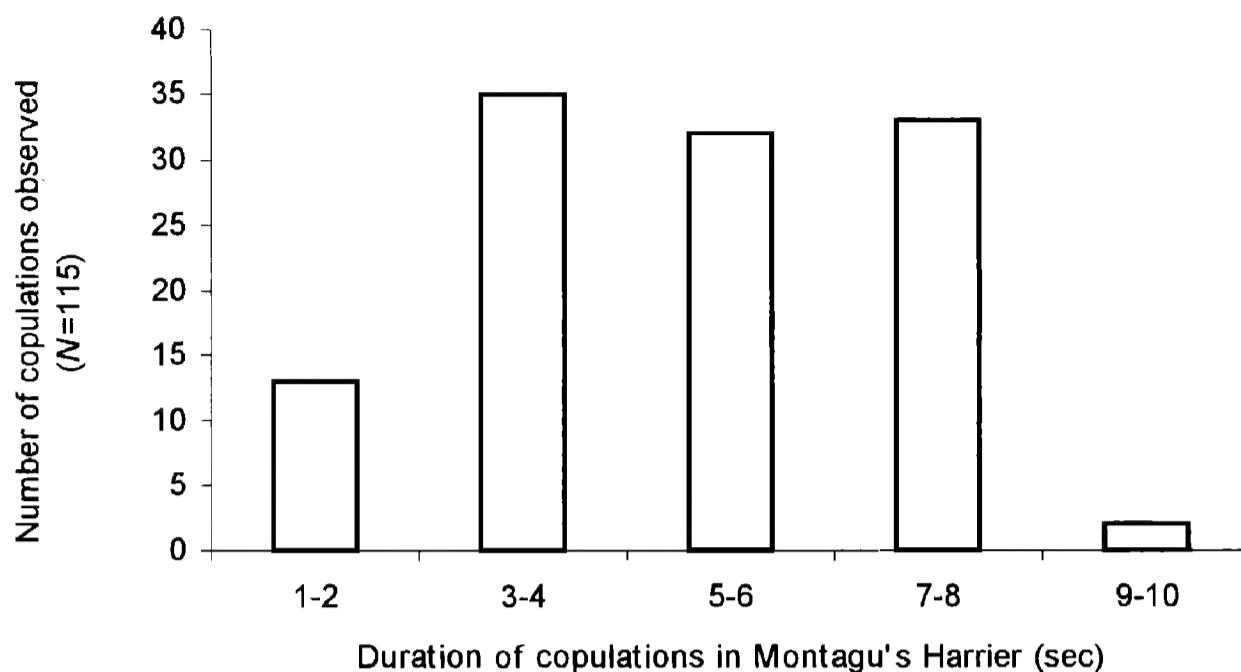


Figure 1. Duration of copulations in Montagu's Harriers in the Pesaro-Urbino area, Italy.

RESULTS AND DISCUSSION

Montagu's Harriers mated on the ground (89% of 111 copulations) and on perches such as poles or shrubs (11%). Prior to copulation, the most frequent activity observed involving both members of the pair was a food pass (48% of 94 cases). In 17% of the cases, the pair had previously performed copulation, while in 5% of the cases there had only been flight play. Males were perched in breeding areas in 14% of the cases and in 28% of the cases for females. Males performed a sky-dance in 1% of

cases, and showed intraspecific aggressiveness in 5% of the cases. In four of these cases, males attacked other males (three neighbors and one not identified) and, on one occasion, a male attacked a female neighbor.

Males flew in front of females and turned sharply (in a hook-flight) to land on their backs. If males came from behind, they simply glided onto the females' backs. Males balanced themselves by stretching out and beating their wings while females lowered and raised their tails to allow cloacal contact.

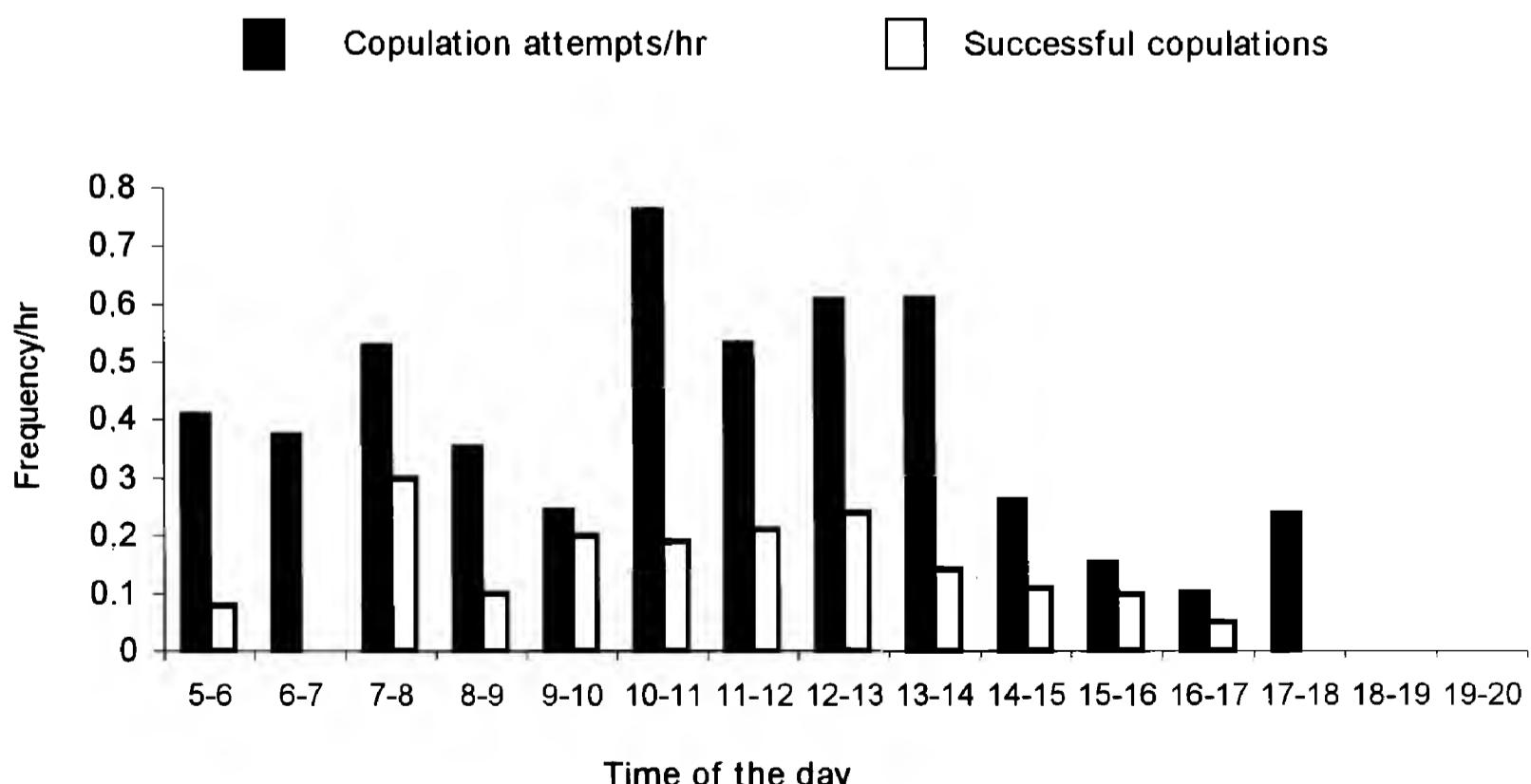


Figure 2. Diurnal fluctuation in frequency of copulation in Montagu's Harriers in the Pesaro-Urbino area, Italy.

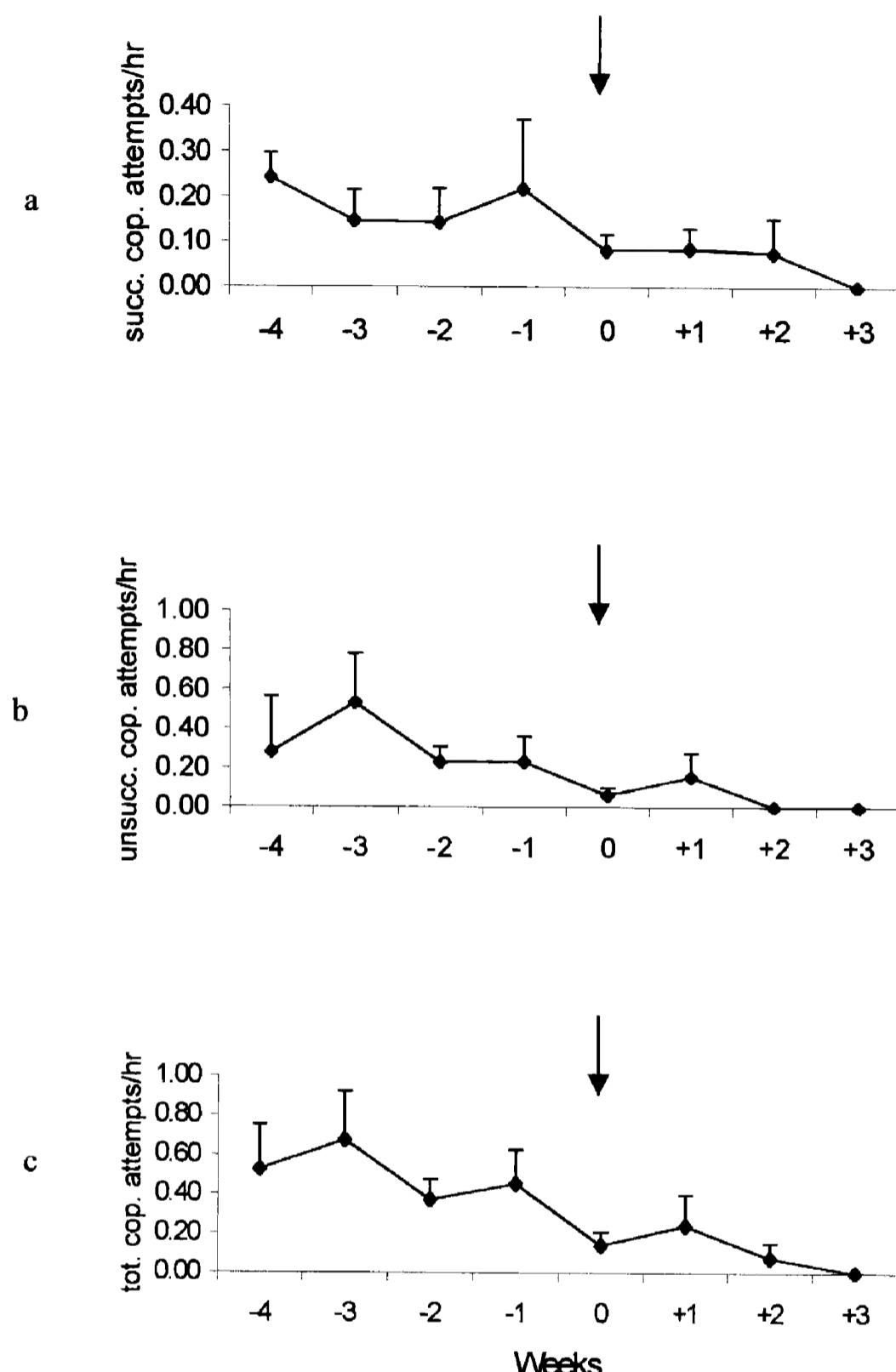


Figure 3. Seasonal variation in successful (a), unsuccessful (b) and total copulation attempts (c), relative to the beginning of egg laying (↓) in Montagu's Harriers in the Pesaro-Urbino area, Italy. Y-axes show means and SE.

The average duration of successful mounts was 4.9 sec (SD = 2.1; $N = 115$) and 87% of 115 copulations lasted between 3–8 sec (Fig. 1). There were no significant differences (Kruskal-Wallis test, $H = 0.1085$, $df = 2$, $P = 0.09$) in the duration of copulations between the three time periods into which we divided the day (dawn–0900 H, 0900–1400 H, and 1400 H–sunset).

Following each copulation, both males and females perched in the area in the majority of 94 cases (53% for males, 69% for females). In 15% of

the cases, there was further copulation. In 21% of these, males left nesting areas while females left in 9%. In the remaining cases, we recorded activities such as intraspecific aggressiveness (3% for males: two cases toward other males and one case toward a female; 2% for females: one case toward another female), flight play (1%), and other behaviors (9% for males, 4% for females).

Copulation attempts occurred unevenly throughout the day ($\chi^2 = 16.10$, $df = 6$; $P < 0.05$), showing a higher frequency between 1000–1400 H.

After 1400 H, there was a marked reduction in copulation frequency, apart from a smaller peak between 1700–1800 H (Fig. 2).

The seasonal trend in copulation attempts carried out by males showed a peak during the courtship period in wk -3 (3 wk prior to the beginning of egg laying) when 0.68 copulation attempts/hr was recorded. Another smaller peak occurred in wk -1, with 0.45 copulation attempts/hr (Fig. 3c). We found a significant difference in the total copulation attempts/hr during the various weeks (Kruskal-Wallis test $H = 17.44$, $df = 7$, $P = 0.0147$) with a constantly decreasing trend from wk 4 to wk +2, after which no further copulation attempts were recorded in the six focal pairs.

The frequency of successful copulations peaked at 0.24 copulations/hr during wk -4, with a second peak of 0.22 copulations/hr during wk -1 (Fig. 3a) but copulation frequency did not vary significantly over time (Kruskal-Wallis test $H = 9.37$, $df = 7$, $P = 0.2271$). Both Goshawks (*Accipiter gentilis*) (Møller 1987) and Lesser Kestrels (*Falco naumanni*) (Negro et al. 1992) show a similar bimodal pre-egg laying peak in copulations.

The frequency of unsuccessful attempts was very high during the courtship period and decreased after wk -1 (Fig. 3b). The variation in frequency between the various weeks was statistically significant (Kruskal-Wallis test $H = 16.13$, $df = 7$, $P = 0.0239$).

During the courtship period (21 d, wk -4, -3, -2) and the presumed female fertile period (13 d for a modal clutch of four), we observed 40 successful copulations during 192 hr of observations, yielding a frequency of 0.2 successful copulations/hr. Considering that daily harrier activity spans 15 hr, each pair ($N = 6$) successfully copulated about 102 times per clutch (range = 31–245). The range was very wide but was comparable with other raptors. In fact, for the African Marsh-Harrier (*Circus ranivorus*), Simmons (1990) estimated 37–160 successful copulations per clutch whereas Birkhead and Lessells (1988) reported a range of 20–97 successful copulations per clutch for Osprey.

Copulations during the courtship period occurred outside the female fertile period. In other species of raptors, copulations have been recorded both during and outside the female fertile period: Goshawks (Møller 1987), Cape Vultures (*Gyps coprotheres*) (Robertson 1986), Ospreys (Birkhead and Lessells 1988), African Marsh-Harriers (Simmons 1990), Merlin (*Falco columbarius*, Shodi 1991),

Lesser Kestrels (Negro et al. 1992) and Black Kites (*Milvus migrans*, Koga and Shiraishi 1994).

Various explanations have been given to explain copulation in the early stages of the breeding season. For example, males may try to copulate early on in the pre-laying period to increase their paternity insurance, given that it is not certain when the female will lay the first egg (Birkhead and Møller 1992). Alternatively, it may be in the female's interest to hide her fertile period to exchange copulations for food (Møller 1987). The latter hypothesis is not very probable for Montagu's Harriers, as there is no relation between the hourly rate of successful copulations and the hourly rate of food passes during these weeks (Spearman correlation coefficients $r_s = 0.1567$, $N = 30$, $P = 0.408$). Another possibility is that copulation attempts at the beginning of the breeding season are part of a evaluation mechanism by females (Tortosa and Redondo 1992). They could also function to establish and maintain the pair bond (Newton 1979), given that Montagu's Harriers remate every year (Cramp and Simmons 1980).

The peak of successful copulations during wk -1 corresponded to the presumed female fertile period and might be explained both by fertilization and sperm competition hypotheses. In fact, most harriers produce unhatched eggs (Simmons 1990) and the six pairs that we studied produced 25 eggs, 20% of which did not hatch. This suggests that frequent copulation limits infertility of eggs while diluting the sperm of other males. Hatching failure might also be due to defects in eggs rather than a lack of sperm, but we do not have information on this possibility.

Given that copulations recorded during the incubation period continued until wk +2, they may function to provide sperm for replacement clutches in the case of nesting failure, as suggested by Birkhead et al. (1987). They may also serve to maintain the pair bond. Because only males engage in play and feeding activity with young during the post-fledging period (Giacchini and Pandolfi 1994, Pandolfi 1996), the pair bond is probably weakened. This could explain why copulations were not recorded later in the breeding season as happens in Cape Vultures (Robertson 1986), Goshawks (Møller 1987) and African Marsh-Harriers (Simmons 1990). For Cape Vultures, pair bonds are lifelong (Robertson 1986) and African Marsh-Harrier pairs bond for >1 yr (Simmons 1990). The Goshawk is a nonmigratory species and pair bonds

certainly last longer than in the migratory Montagu's Harrier.

Of 118 copulations we observed, 4 EPC attempts were observed (3.4%). EPCs involved two extra-pair males, and two females that belonged to focal pairs. Two EPCs occurred 7 d before the start of egg laying, while the other two occurred 2 d before egg laying. All four attempts occurred during females' presumed fertile periods (two females involved). Two of the four EPCs were successful (i.e., the male stayed on the back of the female for ≥ 4 sec). In three of the cases, the female's mate was absent. In the one case when her mate was present, his behavior showed indifference, but the EPC was unsuccessful. Females never rejected the attempts of the extra-pair males and all females were already mated in the colony. One of the males involved already had a mate and belonged to the colony, while the other was not identified. The percentage of EPCs recorded in our study was slightly less than that reported by Arroyo (1996) for Montagu's Harrier in Spain. The fact that the four cases we observed all fell within the presumed female fertile period and that females never resisted suggests that this strategy effectively allows pursuing males, even only occasionally, to increase their reproductive success at the expense of others. Although Simmons (1990) reported an EPC of 2% in African Marsh-Harriers, he found that the males copulated more frequently when they nested in colonies. His finding supports the sperm competition hypothesis suggesting that such a low number of EPCs could trigger mechanisms of sperm competition benefiting those males that use them and take the necessary countermeasures. Montagu's Harrier males spent more time ($\chi^2 = 59.94$, $df = 1$, $P < 0.01$, Yates corrected) in the nesting area near their partner during the female fertile period (43%) than during wk +1, +2, +3 (35%), a pattern that is common in other raptors such as African Marsh-Harriers (Simmons 1990), Ospreys (Birkhead and Lessells 1988) and Goshawks (Møller 1987). Behaving in this way, males may deter access to females by other males (Birkhead and Lessells 1988). This form of male mate-guarding could explain the low proportion of EPCs observed.

For females, the risks regarding the loss of parental care (Trivers 1972) could be minimized if the intruder were to carry out the EPC attempts in the absence of their males, as in fact happened in three out of four cases we observed. The fact that the females did not dissuade these males suggests

that they already knew these males and they were of "high quality." Even though one of the two males was unidentified, it probably belonged to the colony under observation, which comprised five pairs during the reproductive season. The risks could be too high for females accepting EPCs from unknown males since a male of unknown quality could fertilize their eggs (Birkhead and Møller 1992). However, females may gain by increasing the genetic quality or diversity of chicks (Birkhead and Møller 1992). Indeed, numerous cases have been recorded of broods not genetically related to their putative father (Avise 1996). Data available on raptors suggests that this phenomenon is not widespread (Swatschek et al. 1994, Korpimäki et al. 1996, Negro et al. 1996) but is present nonetheless.

In 48% of 94 cases, food passes occurred 5 min before copulations. However, copulation frequency was not correlated with food passes during the first six weeks of the breeding season (Spearman correlation coefficient, $r_s = 0.16$, $N = 30$, $P = 0.4$). There was also no significant correlation between the frequency of successful copulations and food-pass frequency over the various weeks ($r_s = 0.1567$, $N = 30$, $P = 0.408$). These data are similar to those found by Picozzi (1984) for Hen Harriers (*Circus cyaneus*) and by Simmons (1990) for African Marsh-Harriers that showed food passes to be important, but not essential, correlates of copulation. Consequently, we examined whether the duration of a copulation was influenced by the presence of food provided by males. The median duration of copulation attempts when food was present (4 sec) was significantly higher than the median duration of copulation when food was not present (0 sec, Mann-Whitney U -test, $U = 691.5$; $P = 0.01$). This difference remained significant even when only attempts in which males effectively landed on females' backs (food present median = 5 sec; food absent median = 3 sec; $U = 152.5$; $P = 0.0496$).

When food was present, males were successful in 29 out of 56 cases (52%); without food, only 5 out of 35 attempts (14%) were successful ($\chi^2 = 11.39$, $df = 1$, $P < 0.01$, Yates corrected). Of 91 attempts, 56 (62%) were carried out in the presence of food, while 35 (38%) were attempted in the absence of food, a difference that is statistically significant ($\chi^2 = 4.4$, $df = 1$, $P < 0.05$, Yates corrected). Therefore, the duration of copulations was influenced by the presence of food brought by males and they attempted copulations when the probability of success was highest (i.e., when females had received

or were eating prey). For African Marsh-Harriers, Simmons (1990) found that, while food was not a prerequisite for copulation and did not even influence the duration, males had a higher probability of being unsuccessful if food was absent. For Ospreys, Poole (1985) reported that feedings were not an immediate stimulus for copulations but that efficient food transfers among courting Ospreys appeared to be a requirement for successful copulations.

We observed 14 copulation rejections by female harriers in 114 within-pair copulations, 47 (41%) of which were successful. This was considerably lower than the 73% estimated for African Marsh-Harriers (Simmons 1990). The unsuccessful attempts resulted directly from the female's behavior. In the other 53 cases, two of the failures were attributable to external factors (e.g., males left to fight off female intruders or left to fight off crows [*Corvus* spp.]). For the remainder of cases we could not identify the reason for the copulation failure.

Of the 14 cases in which the female refused to copulate, 13 occurred during courtship and only one occurred during fertile period. The possibility that females simply were not physiologically ready is little supported by our data. In fact, from the beginning of the courtship period, we observed successful copulations (Fig. 3). During the daytime, 10 out of 14 refusals were observed between 1000–1400 H, when the frequency of successful copulation attempts/hr was high (Fig. 2). In four cases food was present, in six it was absent, and in the remaining four cases the presence or absence of food was unrecorded. We have no data on prey size in these cases, so we cannot control for any correlation between prey size and female refusal.

We observed the following female behaviors during copulation refusals: in four cases, males had begun landing when females lay flat on the ground keeping their wings semiopen and flattened with their tails toward the ground; in seven cases, females opened and beat their wings; a female flew away once; once a female jumped away; and once a female hit the male with her talons claws while landing. The first behavior was also described by Studinka (1942) as soliciting behavior for copulation by the female. We interpreted this as a refusal because when examining the 13 cases in which females behaved in this way (seven cases observed in two out of the six focal pairs and six cases observed in two other pairs), the male copulated successfully

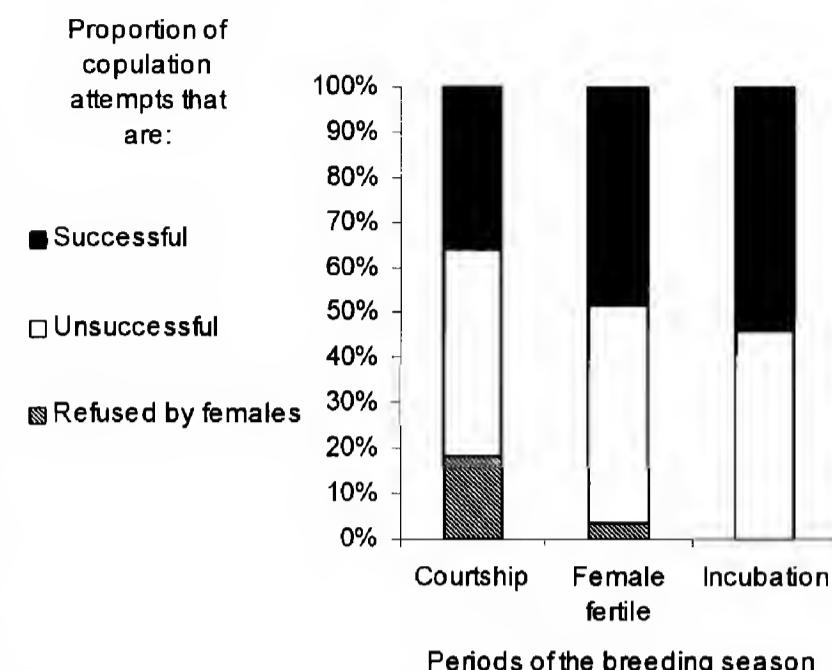


Figure 4. Proportion of successful and unsuccessful copulation attempts and refusal by female Montagu's Harriers during various periods of the breeding season in the Pesaro-Urbino area, Italy.

on only one occasion. Sudden opening of wings by the female followed by flattening on the ground are movements which make it difficult for males to land. The fact that females spread their tails toward the ground could have been a signal indicating unwillingness to copulate since the tail must be raised for cloacal contact.

Even though there was not a significant difference between the proportion of successful copulation attempts, copulation attempts that failed because of refusal by the female, and those that failed for other reasons during the three periods considered ($\chi^2 = 6.71$, $df = 4$, $P > 0.05$) females refused 18% of the attempts by the males during the courtship period and refused only 3% of attempts during their presumed fertile period (Fig. 4). The increase in the proportion of successful copulations during the fertile period appeared to be due, at least in part, to the lower number of female refusals. Simmons (1990) reported nine (4.6%) cases of refusal by female African Harriers out of 196 attempted copulations. This rate is similar to that reported by Koga and Shiraishi (1994) for Black Kites, where 4.1% of 246 copulation attempts were refused by females. In both cases, however, the periods in which refusals took place were not reported.

In White Storks (*Ciconia ciconia*, Tortosa and Redondo 1992) and Lesser Kestrels (Negro et al. 1996), males copulate frequently even in the absence of sperm competition. It has been suggested

that these males may advertise their good condition by performing energetically costly copulations; therefore, copulations are part of a process of mate assessment involved in the acquisition and maintenance of the pair bond (Tortosa and Redondo 1992, Negro et al. 1996). This may also be the case in the Montagu's Harrier. Intense copulation activity carried out by males despite female refusals could serve to indicate the general health of males, assuming that copulations are expensive in terms of sperm production and physical courtship activity (Dewsbury 1982). Furthermore, in refusing, females could test the ability of males to copulation and fertilization. A rather long period would be advantageous to establish the quality of males in order to limit the risks of being deceived. If these characteristics were inherited, it would be advantageous for females to fertilize her eggs with these males (Birkhead and Møller 1992).

In conclusion, while the frequent copulation pattern observed in Montagu's Harrier may be explained with the sperm competition hypothesis, copulations may also have an important social function during the courtship period. For females, it could be a way of evaluating the quality of males. Therefore, refusal is an aspect of female behavior that could help us to understand if, and in what way, female choice is based on the capacity of males to transfer sperm.

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SEX IDENTIFICATION IN RAPTORS USING PCR

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ABSTRACT.—Recent discovery of a gene on the W-chromosome of birds provides a method for sexing in a variety of avian taxa. We investigated the possible use of polymerase chain reaction (PCR) primers specific to the CHD-W (chromodomain-helicase-DNA-binding on the W-chromosome) gene to identify sex in nine species of raptors. Blood was collected from birds of known-sex (female and male) and DNA was extracted. PCR, using primers P2 and P3, was performed followed by restriction enzyme digestion of the PCR products. Primers P2 and P3, specific to the CHD genes, reliably confirmed the sex in all 38 birds tested representing nine species and four families. A convenient, inexpensive and effective procedure was developed for blood collection, storage and subsequent DNA isolation and PCR analysis.

KEY WORDS: *CHD gene, sex identification; raptors, W-chromosome, PCR.*

Identificación de sexo en aves rapaces mediante la utilización de la RCP

RESUMEN.—El reciente descubrimiento de un gene en los cromosomas W de las aves es un metodo para sexar una variedad de taxones aviares. Hemos investigado el posible uso de la reacción de la cadena polymersa (RCP) con el fin de identificar el sexo en nueve especies de rapaces. Muestras de sangre fueron obtenidas de seis aves de las cuales se conocía su sexo (machos y hembras), el ADN fue extraido. La RCP fue obtenida mediante la utilización de P2 y P3 y la restricción de la enzima digestiva de los productos de la RCP. Este método permitió, en forma confiable identificar el sexo en las 30 aves, las cuales representaban nueve especies y cuatro familias. Un método conveniente y poco costoso fue desarrollado para la recolección de muestras de sangre, almacenaje y el subsecuente aislamiento del ADN y el análisis de la RCP.

[Traducción de César Márquez]

The identification of sex is often a problem when studying raptors because sexes are not distinct morphologically. This problem is especially true in juveniles and hatchlings. One effective solution is to exploit DNA markers to diagnose sex. Birds show female heterogamety in having one W- and one Z-sex chromosome whereas males have two Z-chromosomes. Because of this, a simple polymerase chain reaction (PCR) technique can be used to identify sex across a broad range of bird taxa at any stage of development (Griffiths et al. 1996). PCR is a robust technique which can target and amplify specific sequences of DNA (Mullis and Faloona 1987). The PCR primers, P2 and P3, amplify a highly conserved region on the W-sex chromosome known as the CHD (chromodomain-helicase-DNA-binding) gene. A second version of the CHD gene (CHD-NW), not W-linked, is also amplified by the primer pair and is present in both female and male birds. Recently, CHD-NW has been shown to be linked to the Z-chromosome in chickens (Griffiths and Korn 1997). This finding

indicates that, among a wide variety of bird species, amplification using the single set of PCR primers followed by restriction digestion of the PCR products will allow for discrimination between the presence of the W-linked CHD gene (unique to female birds) and the CHD-NW gene. A specific restriction enzyme will cut the CHD-NW amplification product but not the W-linked version. The presence/absence of a 110 base pair (bp) band, following enzyme digestion, is diagnostic for sex identification in all bird species previously tested (Griffiths et al. 1996). Our objective for this study was to determine the reliability of PCR primers P2 and P3 in the sexual identification of a variety of raptors.

MATERIALS AND METHODS

Blood was collected from 38 individuals of known-sex from each of the following species: Bald Eagle (*Haliaeetus leucocephalus*), Red-tailed Hawk (*Buteo jamaicensis*), Red-shouldered Hawk (*Buteo lineatus*), Osprey (*Pandion haliaetus*), American Kestrel (*Falco sparverius*), Merlin (*Falco columbarius*), Black Vulture (*Coragyps atratus*), Barred Owl (*Strix varia*) and Great-horned Owl (*Bubo virginianus*).

The sex of each bird was determined through necropsy, reproductive behavior and/or morphometric and behavioral data. Blood was drawn from the brachial vein of the wing using a 1–3 ml syringe with a 22–25 gauge needle (depending on the species) after swabbing the area with alcohol. Approximately 100 μ l of blood was transferred from the syringe to a heparinized microhematocrit tube (Becton Dickinson, Franklin Lakes, NJ U.S.A.) for DNA extraction purposes. Both ends of the tube were plugged with microhematocrit tube sealer (Becton Dickinson). The microhematocrit tube was stored at 4°C for one day to several weeks prior to DNA extraction. If longer storage was required, tubes were placed at –20°C.

DNA was extracted from whole blood using InstaGene Whole Blood Kit (BioRad, Hercules, CA U.S.A.) according to manufacturer's protocol with the following modifications. Five microliters of whole blood per sample were added to a 1.5 ml microcentrifuge tube containing 1 ml of the supplied lysis buffer. The tube was incubated 8–15 min at room temperature and the supernatant discarded. The remaining pellet was washed twice with lysis buffer, carefully removing the supernatant each time. Two hundred microliters of InstaGene matrix was added to the pellet and the tube incubated 8 min at 70°C. The sample was then vortexed, incubated at 95°C for 4 min and centrifuged (15 000 rpm) for 1 min. The resulting supernatant was stored at –20°C per kit instructions until used in PCR analysis.

Standardized PCR reactions were performed twice on DNA from all birds using a 96-well microtiter plate format (Falcon) in a MJ Research Model PTC-100 Programmable DNA Thermal Controller to determine repeatability of PCR reaction conditions. A PCR reaction volume of 20 μ l per sample contained: 1× *Taq* DNA polymerase buffer, 200 μ M each dNTPs, 3.5 mM MgCl₂, primers P2 (5'TCTGCATCGCTAAATCCTT3') and P3 (5'AGATATTCCGGATCTGATAGTGA3') (National Biosciences, Inc., Plymouth, MN U.S.A.) at 1 μ M each, 100–200 ng of genomic DNA (5 μ l of DNA extraction reaction) and 0.5 units of *AmpliTaq* DNA polymerase (Perkin Elmer, Foster City, CA U.S.A.). Cycling parameters were 94°C for 1.5 min, followed by 56°C for 15 sec, 72°C for 15 sec, 94°C for 30 sec, for 30 cycles and one cycle of 56°C for 1 min and 72°C for 5 min. Negative controls containing water were run with every PCR and precautions were taken to avoid contamination (Thomas and Paabo 1993).

Following PCR, all samples were subjected to restriction enzyme digest with *HaeIII*. Five units of *HaeIII* (New England Biolabs, Beverly, CA U.S.A.) were used to cut 7 μ l of each PCR reaction following manufacturer's recommendations for appropriate buffer and temperature. Restriction enzyme digestion reaction components were prepared as a master mix to ensure consistent results across all samples.

Samples were electrophoresed on a 2.0% agarose gel (1:1 Amersham Life Sciences, Arlington Heights, IL U.S.A.; Life Technologies, Gaithersburg, MD U.S.A.) at 100 V for 1–2 hr in 1× TBE buffer (90 mM Tris-borate, 2 mM EDTA pH = 8.0) followed by staining for 20 min in 0.5 μ g/ml ethidium bromide solution (Maniatis et al. 1982).

RESULTS

For all species tested in this study, primers P2 and P3 produced PCR products of 110 bp in size in both female and male birds. These primers are specific to both versions of the CHD gene, CHD-W, on the W-chromosome (unique to females) and CHD-NW on a non-W-chromosome (present in both sexes) (Griffiths et al. 1996, Ellegren 1996). This results in the presence of two PCR fragments in females, both 110 bp in size. Males have only one fragment type, CHD-NW. Digestion of the CHD-NW product with a restriction enzyme allows for discrimination between the two PCR products and the determination of sex. The restriction enzyme *HaeIII* was used to cut the CHD-NW product (into two fragments of 45 bp and 65 bp); the CHD-W product remained intact (Fig. 1). For 34 birds, the sex of each was correctly identified by the PCR/*HaeIII* enzyme digest reaction. *HaeIII* did not digest the CHD-NW products for the four Barred Owl samples. This PCR product was subsequently isolated from a known-male sample and sequenced. The sequence data revealed the loss of the *HaeIII* site and provided a candidate *MboII* site for testing. Upon testing in four known-sex samples, *MboII* provided accurate discrimination between female and male samples.

DISCUSSION

We found that PCR primers P2 and P3 located on the CHD genes of birds reliably sexed the raptors we studied. Primers P2 and P3 confirmed the sex in all 38 species of raptors sampled representing nine species and four families. Other molecular methods have been used to sex raptors but are not useful across taxa and can be a challenge in terms of technique and resources (Longmire et al. 1991, May et al. 1993). PCR is a more straightforward, less labor-intensive technique and more amenable to implementation in less technical settings.

Our study developed a convenient, inexpensive and effective procedure for blood collection, storage and subsequent DNA isolation. Blood is collected in heparinized microhematocrit tubes that can be stored at 4°C for several weeks prior to DNA extraction and still yield viable, high molecular weight DNA. Preparation of DNA from whole blood using a commercial DNA extraction kit expedited the procedure and eliminated the use of hazardous reagents. The PCR protocol works well in a 96-well format allowing for the processing of a large number of samples at one time. Although



Figure 1. PCR products and corresponding *HaeIII* enzyme digests from one known female and one known male from six of nine raptor species evaluated. For each species (RTHA = Red-tailed Hawk; RSHA = Red-shouldered Hawk; GHOW = Great Horned Owl; BLVU = Black Vulture; BAEA = Bald Eagle; OSPR = Osprey), the first two lanes (1 and 2) represent the one female sample; the next two lanes (3 and 4) represent the one male sample. Lanes 1 and 3 show the 110 bp PCR products generated using primers P2 and P3. Lanes 2 and 4 show the results from the *HaeIII* enzyme digestion. The 'std' lanes contain a 100 bp molecular weight size standard (Life Technologies).

blood was the tissue source for DNA in this study, the sensitivity and specificity of the PCR technology should allow for the use of other tissue sources such as feathers. Based on the fact that sex identification was not shown through the use of a single enzyme (*HaeIII*) for every species tested in this study (Barred owl required *MboII*), known-sex birds from untested species could be initially evaluated using a panel of restriction enzymes. Griffiths et al. (1996) suggested several enzymes that appear to be appropriate over a broad range of avian families and would provide a reasonable starting point. Future modifications of this technique to include primers to the CHD genes that amplify across an intron may eliminate the need for restriction enzymes in some species (Ellegren and Shelton 1997).

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HEMATOLOGY AND HEMATOZOA OF ADULT AND NESTLING COOPER'S HAWKS IN ARIZONA

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ABSTRACT.—We determined age- and sex-specific packed cell volume (PCV) and total blood solid (TS) levels to detect diseases in Cooper's Hawks (*Accipiter cooperii*) in southeast Arizona. We also identified hematozoa infecting Cooper's Hawks, determined age- and sex-specific infection rates, and evaluated the influence of hematozoan infections on PCV and TS. Adult male Cooper's Hawks had greater mean PCVs than adult females and nestlings ($P < 0.05$). Adult females also had a greater mean PCV than nestlings ($P < 0.05$). There was no difference in PCV between the sexes of nestlings and there was no difference in TS levels between the sexes of adults or nestlings, but TS levels were greater among adults ($P < 0.05$). Hematozoan infection rates did not differ between the sexes of adults ($P = 0.553$) but adults had a greater infection rate than nestlings ($P = 0.022$). Hematozoan infections did not appear to influence PCV or TS among adult Cooper's Hawks.

KEY WORDS: *Cooper's Hawks; Accipiter cooperii; Arizona; blood parasites; hematolgy; hematozoa.*

Hematología y hematozoarios en pichones y adultos de *Accipiter cooperii* en Arizona

RESUMEN.—Determinamos el volumen de células específicas compactadas de edad y sexo, y el total del nivel de sólidos de sangre para detectar las enfermedades de *Accipiter cooperii* en el sudeste de Arizona. También identificamos los hematozoarios que infestan a *Accipiter cooperii*, mediante la determinación de las tasas de infestación por sexo y edad. Evaluamos la influencia de los hematozoarios en las células compactadas y en el total de sólidos de sangre. El macho adulto de *Accipiter cooperii* tuvo una media mayor de células compactadas que las hembras adultas y que los pichones ($P < 0.005$). No hubo diferencias de células compactadas entre sexos de pichones como tampoco en los niveles del total de sólidos de sangre entre sexos de adultos o pichones, pero los niveles de sólidos de sangre fueron mayores entre adultos ($P < 0.05$). Las tasas de infección de hematozoarios no difirieron entre sexos de adultos ($P = 0.553$), pero los adultos tuvieron una tasa de infestación mayor que los pichones ($P = 0.022$). Las infestaciones por hematozoarios aparentemente no influenciaron las células compactadas o los sólidos de sangre en los adultos de *Accipiter cooperii*.

[Traducción de César Márquez]

Two hematological variables often measured when evaluating the health of birds are packed cell volume (PCV) and total solids (TS) or the protein concentration in the plasma (Campbell 1988). Few studies have investigated these hematological parameters for Cooper's Hawks (*Accipiter cooperii*)

(Smith and Bush 1978, Hunter and Powers 1980, Gessaman et al. 1986), nor have differences between adults and nestlings or among birds with concomitant parasitic infections been investigated.

Studies of the hematozoa of North American raptors have been primarily conducted in the eastern and midwestern U.S. (Stabler and Holt 1965, Kocan et al. 1977, Kirkpatrick and Lauer 1985, Taft et al. 1994), but the occurrence of parasitic hematozoa appears to vary regionally (Greiner et al.

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1975). Evaluation of hematozoa infection rates among Cooper's Hawks has been hampered by the tendency of investigators to pool blood samples from all individuals regardless of age, season in which samples were taken, or whether they were free-ranging or captive. In a notable exception, Taft et al. (1994) evaluated infection rates of hematozoa among Cooper's Hawks on basis of sex and age during the breeding season.

We obtained blood samples from adult, subadult and nestling Cooper's Hawks while conducting a demographic study of the species in southeastern Arizona (Boal 1997). We analyzed blood samples to determine age- and sex-specific PCV and TS values for Cooper's Hawks, to identify hematozoa and hematozoan infection rates, to examine possible influences of hematozoan infections on PCV and TS, and to compare hematozoan infection rates between our study and a similar study in Wisconsin (Taft et al. 1994).

MATERIALS AND METHODS

We collected blood samples from breeding and nestling Cooper's Hawks in southeastern Arizona, primarily in the vicinity of Tucson, Arizona ($32^{\circ}15'N$, $111^{\circ}55'W$) from May–June 1995 (Boal 1997). We captured breeding hawks with dho-gaza and bal-chatri traps (Bloom 1987); nestlings were captured by hand at nests. The pronounced sexual size dimorphism in Cooper's Hawks (Snyder and Wiley 1976) facilitated sexing of both adults and nestlings. We collected blood samples within 15 min of capture by drawing 0.25 ml of blood from the basilic vein with a 25-gauge nonheparinized needle and 3-ml syringe. Each sample was immediately transferred to an EDTA 0.3-ml tube and refrigerated for transport from the field.

We used the microhematocrit method to determine PCV. We centrifuged blood samples in nonheparinized microhematocrit tubes and determined the PCV by taking the average value of two samples from each hawk. TS values were determined by analyzing plasma samples with a No. 33077 Schuco Clinical Refractometer.

To examine the prevalence of hematozoa in Cooper's Hawks, we made two thin smears of each blood sample on glass slides. The slides were air-dried, fixed in methanol, stained in Giemsa, and microscopically examined at $1000\times$ for hematozoa. The entire blood smear was examined for all samples. We also compared our results to data from Wisconsin (Taft et al. 1994) to examine age- and sex-specific hematozoa infection rates of Cooper's Hawks from northern and southern parts of their breeding range.

We used *t*-tests and one-way analysis of variance tests (Ramsey and Schafer 1997) to examine differences in PCV and TS between adult and nestling Cooper's Hawks, between males and females in each age class, and to examine the influence of hematozoa on PCV and TS. We report means and standard errors for PCV and TS levels. Subadult Cooper's Hawks that were members of breeding pairs were pooled with adults for our analyses. When necessary, we logarithmically transformed data to meet as-

Table 1. Packed cell volume (PCV) and total solids (TS) for free-ranging adult and nestling Cooper's Hawks in southeastern Arizona in 1995.

AGE/SEX	N	PCV	SE	TS	SE
Adult ♀ ♀	35	50.7	0.64	4.13	0.10
Adult ♂ ♂	26	53.7	0.51	4.02	0.06
Nestling ♀ ♀	8	42.2	1.16	3.15	1.70
Nestling ♂ ♂	5	38.7	1.04	3.12	0.16

sumptions of normality and equal variance. If transformations failed, we used Mann-Whitney rank sum tests and Kruskal-Wallis one-way analysis of variance on ranks (Ramsey and Schafer 1997). We used chi-square contingency tables with Yates correction for continuity (Ramsey and Schafer 1997) to compare hematozoa infection rates between sexes of adults, between adults and nestlings, and between regions. We used Fisher's exact test (Ramsey and Schafer 1997) when small cell counts violated assumptions of a contingency table. Statistical analyses were conducted with the SigmaStat statistical package version 1.0.

RESULTS

We collected blood samples from 61 adult and 28 nestling Cooper's Hawks. Data for PCV and TS of 15 of these nestlings were excluded due to *Trichomonas gallinae* infections (Boal et al. 1998) that could have biased results. We found that PCV levels varied significantly among the ages and sexes of Cooper's Hawks ($F_{3,70} = 46.7$, $P < 0.001$; Table 1). A pairwise multiple comparison procedure indicated adult males ($\bar{x} = 53.7 \pm 0.51$) and adult females ($\bar{x} = 50.7 \pm 0.64$) had greater mean PCVs than nestling males ($\bar{x} = 42.2 \pm 1.16$) or nestling females ($\bar{x} = 38.7 \pm 1.04$, $P < 0.05$; Table 1). Adult males also had a greater mean PCV than adult females ($P < 0.05$) but there was no difference in mean PCV between nestling males and nestling females (Table 1). We found that TS levels also varied among the age and sex categories of Cooper's Hawks ($H_3 = 24$, $P < 0.001$; Table 1). A pairwise multiple comparison showed that age was the source of variability in TS levels. There was no difference between adult males ($\bar{x} = 4.02 \pm 0.06$) and females ($\bar{x} = 4.13 \pm 0.10$) or between nestling males ($\bar{x} = 3.12 \pm 0.16$) and females ($\bar{x} = 3.15 \pm 1.70$), but adults had greater mean TS levels than nestlings ($P < 0.05$; Table 1).

We examined blood smears of 44 breeding and 18 nestling Cooper's Hawks for the presence of parasitic avian hematozoa. Infection rates were not different between the sexes of adult hawks ($\chi^2_1 = 0.351$, $P = 0.553$) but rates were greater among

Table 2. Hematozoa infection rates of Cooper's Hawks in southeastern Arizona in 1995 in relation to age and sex.

AGE/SEX	N	N_I (%)	N_L (%)	N_H (%)	N_P (%)
Adult ♂♂	17	8 (47)	1 (6)	8 (47)	1 (6)
Adult ♀♀	27	9 (33)	3 (11)	8 (30)	4 (15)
Nestling ♂♂	6	0 (0)	0 (0)	0 (0)	0 (0)
Nestling ♀♀	12	1 (8)	1 (8)	0 (0)	0 (0)
Total	62	18 (29)	5 (8)	16 (26)	5 (8)

N_I = number infected; N_L = *Leucocytozoan*; N_H = *Haemoproteus*; N_P = *Plasmodium*.

adults (39%) than nestlings (5%) ($\chi^2_1 = 5.27, P = 0.022$; Table 2). We identified *Leucocytozoan toddi* (as per Greiner and Kocan 1977), *Haemoproteus* spp., and *Plasmodium* spp. among the samples. All three hematozoa were found in two (4%) of the breeding Cooper's Hawks (Table 2).

There was no relationship between PCV and presence of hematozoa among adult females ($t_{25} = 0.862, P = 0.417$) or males ($t_{15} = 0.227, P = 0.823$), nor was there a relationship between TS and presence of hematozoa among adult females ($U = 114.0, P = 0.554$) or males ($t_{15} = 0.434, P = 0.671$). A low infection rate prevented us from evaluating the influences of hematozoa on PCV and TS of nestlings.

Overall hematozoan infection rates were lower among breeding Cooper's Hawks in Arizona (38.6%) than in Wisconsin (98.6%, Taft et al. 1994) ($\chi^2_1 = 5.55, P = 0.018$). Cooper's Hawks in Arizona had lower infection rates of *Haemoproteus* spp. ($\chi^2_1 = 4.87, P = 0.027$) and *L. toddi* ($\chi^2_1 = 58.5, P < 0.001$) than in Wisconsin. *Plasmodium* spp. was not encountered in Wisconsin, but was detected in 11.3% of the Cooper's Hawks sampled in Arizona (Table 2). Hematozoan infection rates were low among nestling Cooper's Hawks in both Arizona (5%) (Table 2) and Wisconsin (12%) (Taft et al. 1994) (Fisher's exact test, $P = 0.65$).

DISCUSSION

Smith and Bush (1978) suggested PCVs are consistent among raptors, but other studies indicate the parameter is highly variable (Balasch et al. 1976, Hunter and Powers 1980, Rehder et al. 1982, Rehder and Bird 1983, Redig 1993). This may be due in part to differences in hematology between free-ranging and captive raptors (Gessaman et al. 1986, Powers et al. 1994). Among free-ranging *Accipiter* hawks, we found PCV levels for breeding

Cooper's Hawks were slightly higher than those for migrating Cooper's Hawks and Sharp-shinned Hawks (*A. striatus*) (Gessaman et al. 1986, Powers et al. 1994) and similar to wintering Northern Goshawks (*A. gentilis*) (Hunter and Powers 1980).

Breeding male Cooper's Hawks had consistently higher PCVs than adult females. In contrast, there were no differences between the sexes of migrating Cooper's Hawks and Sharp-shinned Hawks (Gessaman et al. 1986, Powers et al. 1994). This may be due to breeding males having higher androgen levels (Domm 1964, Rehder et al. 1982) which cause an increase in red blood cell production and thus PCV. Estrogen levels in female birds caring for young can be quite variable depending on the species. Estrogen causes bone marrow suppression in some animals and, if elevated in female Cooper's Hawks during the nesting cycle, could cause a decrease in their PCV. An elevated PCV and/or TS may be indicative of dehydration (Smith and Bush 1978) but all adult hawks in our study had an apparently unlimited access to water at riparian streams, ponds, bird baths, and other anthropogenic sources of water (Boal 1997).

Cooper's Hawk nestlings had PCV levels 17% (females) and 28% (males) lower than adults. Similarly, the PCV of nestling Red-tailed Hawks (*Buteo jamaicensis*) is 26% lower than the PCV of adults (Redig 1993). The lower PCV values of the nestling Cooper's Hawks may represent a normal preadult hematological status as is documented in many animals (Jacobson and Kollias 1988). Lower preadult PCV levels may result when young hawks are under stress (e.g., sibling competition for food or nest crowding). Stress stimulates production of adrenocorticotropic hormone, which in turn stimulates the adrenal gland to produce steroids such as corticosterone and cortisol (Harvey et al. 1986) which may reduce PCV. Another possible explanation is that nestling Cooper's Hawks may have smaller RBCs than adults, as is seen in some other avian species (Jacobson and Kollias 1988). Thus, nestlings and adults may have similar RBC counts, but the smaller cell size in nestlings results in lower PCV. We did not determine red blood cell numbers of either age group in our study.

Age-specific levels of thyroid activity could also explain PCV differences among Cooper's Hawks. Ronald and George (1988) demonstrated that increased thyroid activity in four races of Canada Geese (*Branta canadensis*) was correlated with higher red blood cell counts and PCV. McNabb et al.

(1984) found thyroid activity in quail and doves did not reach adult levels until postfledging. Nestling Cooper's Hawks may likewise have lower thyroid hormone levels and, thus, lower PCV levels.

Haemoproteus spp. has been identified as the most commonly detected avian hematozoan in infected wild birds (67%), with *Plasmodium* spp. (41.5%) and *L. toddi* (39%) occurring in similar frequencies (Bennett et al. 1982). We found all three of these hematozoan parasites in Cooper's Hawks in southern Arizona, but they did not appear to affect PCV or TS. Prevalence of *Haemoproteus* spp. and *L. toddi* were lower in Arizona than in Wisconsin. This difference may have been due to the life cycle of vectors. For example, black flies (*Simuliidae*), the vector of *L. toddi*, require running water to complete their life cycle. Running water is rare in the desert southwest, possibly decreasing the potential for spread of *L. toddi*.

We did not quantify the severity of infections (i.e., percentage of infected red blood cells) but, subjectively, they appeared mild. The single exception was a nestling that was heavily parasitized by *L. toddi*. Our data are from only one breeding season, but it appears hematozoa infections among Cooper's Hawks in southern Arizona are less prevalent than in more northern parts of their range.

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EGESTION OF CHITIN IN PELLETS OF AMERICAN KESTRELS AND EASTERN SCREECH OWLS

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ABSTRACT.—In studying the digestibility of chitin by American Kestrels (*Falco sparverius*) and Eastern Screech Owls (*Otus asio*), we found portions of ingested chitin not only occurred in excreta but also in pellets. When commercial chitin was fed with turkey or chicken meat, 23.8% (American Kestrel) and 29.6% (Eastern Screech Owl) of the ingested chitin was egested in pellets. In American Kestrels, 59.2% of the total amount of ingested chitin was found in excreta. The percent of chitin egested as pellets as compared to the amount ingested showed a negative correlation ($r = -0.76$, $P < 0.001$). Our results suggest that the lower gastrointestinal tract contributes to total chitin digestion in American Kestrels.

KEY WORDS: *American Kestrel; Falco sparverius; Eastern Screech Owl; Otus asio; chitin; digestibility; pellet egestion.*

Residuos de queratina en egragópilas de *Falco sparverius* y *Otus asio*

RESUMEN.—Al estudiar la digestibilidad de la queratina en *Falco sparverius* y *Otus asio*, encontramos que las porciones de queratina ingerida no solo ocurren en las excretas si no que también en las egragópilas. Cuando la queratina de uso comercial fue suministrada con carne de pavo o pollo 23.8% (*Falco sparverius*) y 29.6% (*Otus asio*) este fue eliminado en las egragópilas. En *Falco sparverius*, 59.2% del total de queratina ingerida fue encontrada en las excretas. El porcentaje de queratina eliminada en las egragópilas comparado con el ingerido mostró una correlación negativa ($r = -0.76$, $P < 0.001$). Nuestros resultados sugieren que el tracto gastrointestinal bajo contribuye a la digestión total de queratina en *Falco sparverius*.

[Traducción de César Márquez]

Insect exoskeletons are poorly digested by predators (Kramer and Koga 1986). This is due to the indigestibility of chitin (poly [β -(1-4)-2-acetamido-2-deoxy-D-glucopyranose]) which gives strength and structure to the exoskeleton (Roberts 1992). In spite of its indigestibility, insect chitin is considered a possible dietary source of carbohydrate for predators (Jeuniaux and Cornelius 1978, Weiser et al. 1997).

Eastern Screech Owls (*Otus asio*) and American Kestrels (*Falco sparverius*) are partially or primarily insectivorous (Johnsgard 1988, 1990). When coarse chitin powder was fed, portions were not only found in excreta but also in egested pellets. Chitin egested in pellets is not exposed to digestive enzymes in the lower gastrointestinal (GI) tract where chitinolytic enzymes are found (Jeuniaux 1963). If the lower GI tract contributes to chitin digestion, chitin digestibility would be expected to be higher when all ingesta pass through the whole GI tract.

In this study, we determined the proportion of

ingested chitin that was egested in pellets by captive Eastern Screech Owls and American Kestrels. We also determined the chitinolytic capacity of the lower GI tract in American Kestrels by comparing chitin digestibility in two different cases with and without the egestion of chitin in pellets.

METHODS

Four Eastern Screech Owls and three American Kestrels were used. All individuals were permanently crippled but otherwise healthy. Birds were kept separately in wooden chambers (45 cm wide, 48 cm high and 45 cm deep) in an environmentally controlled room (20–22°C, 40–50% relative humidity and 12 hr of light per 24 hr). Between experiments, the birds were fed whole laboratory mice (*Mus musculus*) daily totaling approximately 20% of each bird's body weight at 1700 H for screech owls and at 1200 H for kestrels. The birds have access to mice until the cages were cleaned the next morning.

Pellets consisting of coarse chitin powder were collected in the process of determining chitin digestibility for kestrels or during the period of acclimating screech owls to a chitin-rich diet. For our experiments, we used commercially available chitin (from crab shell, practical grade, Sigma Chemical, St. Louis, MO, U.S.A.). Chitin

content in this product was determined by crude fiber determination (Helrich 1990) to be 68.5% of the weight of the product.

After acclimation to a diet of chicken or turkey meat for 8 d, kestrels were fed an amount of chitin equivalent to 2% (by weight) of their total dried food (2% chitin diet) at the start of each experiment to determine chitin digestibilities. The day before chitin was fed, all excreta were collected and analyzed for chitin content as a control. Chitin was packed in small pieces of meat. Each piece was fed by forceps to each bird to ensure that all the chitin was consumed. During the experiments, the birds were kept on a chicken or turkey meat diet which amounted to 18% of each bird's body weight (wet weight) daily. The chicken and turkey meat each contained 27.7% dry matter.

Following the feeding of chitin, all excreta and pellets, if egested, were collected from kestrels daily for 2 d on a polyethylene sheet set on a stainless steel pan in the bottom of each cage. Collected excreta and pellets were separately dried at 50°C for 2 d, weighed and finely ground with a pestle and mortar to pass through a 0.5 mm mesh. These ground samples were analyzed to determine their chitin contents. When we fed screech owls 144.5–170.1 mg of chitin with each feeding, they did not egest pellets. However, when we increased the amount of chitin to 300 mg, they egested pellets. Due to this, we fed each screech owl 300 mg of chitin either in turkey or chicken meat (chitin diet, total 15 g) each day for 6 wk to determine whether acclimation to chitin improved chitin digestibility. During this acclimation period, we also fed the birds mice at night to ensure a proper nutrient supply. The chitin diet was fed to screech owls in the afternoon after the birds egested pellets from mice consumed the night before. On many occasions, the owls did not eat the mice until they egested pellets from the chitin diet. These pellets, which consisted of only coarse chitin powder, were dried at 50°C for 2 d and weighed. Ten pellets were ground and prepared for the determination of their chitin content. No excreta were collected; therefore, chitin digestibilities were not determined.

Kestrels were acclimated the same way, but they tended to eat mice before they egested pellets from the chitin diet. As a result, kestrels egested a mixture of chitin powder and mouse fur as pellets. Since both chitin and hair are detected as crude fiber, determination of chitin contents was not possible by the crude fiber determination used when mouse fur contaminated the pellets. Therefore, no useful pellets were collected from kestrels during the acclimation period.

Chitin content was estimated by using the method for crude fiber determination in animal feeds (Helrich 1990). This method was used to estimate chitin contents in arthropods by Jackson et al. (1992), Nicholson et al. (1996), and Weiser et al. (1997). Since the ground excreta and pellets of kestrels were mixed and analyzed together to obtain their chitin contents in our previous study, six extra chitin pellets were collected from kestrels by feeding a 2% chitin diet to determine the chitin content of pellets. A mean of 69% (by dry weight) of the pellet was chitin in kestrels. Similarly, 10 pellets from screech owls were analyzed and found to have a mean of

68% chitin (dry weight). These values were used to calculate the dry weight of chitin in chitin pellets.

Chitin digestibilities of kestrels were determined by comparing the weight of chitin fed to the weight found in excreta and pellets (if egested). Because this method did not consider chitin retained in the GI tract (not immediately excreted), the chitin digestibilities obtained were referred to as "apparent" chitin digestibilities (Jackson et al. 1992). Chitin egested as pellets was not exposed to the possible chitinolytic enzymes in the lower GI tract. Therefore, we calculated means of chitin digestibilities separately in the two different cases (i.e., with or without egestion of pellets). Apparent chitin digestibilities were calculated based on the ratio of assimilation to ingestion and the ratio were converted to percentages of chitin assimilated to chitin ingested. Chitin ingestion and assimilation calculations were based on either the total dry weight of chitin ingested and excreted, or egested. Similarly, the percent of chitin egested in pellets was based on the total dry weight of chitin in pellets.

A pooled *t*-test (Devore and Peck 1993) was used for comparison of apparent chitin digestibilities with or without chitin pellets. An *F*-test was used to obtain a *P* value for correlation coefficients (Devore and Peck 1993). When *P* < 0.05, statistical comparisons were considered significantly different.

RESULTS AND DISCUSSION

Fourteen pellets were collected from three kestrels. No pellets were egested following three chitin feedings in two kestrels. The percent of chitin egested in a pellet relative to ingested chitin was $23.8\% \pm 11.0\%$ (\pm SD) by weight (Table 1). Of total ingested chitin, $59.2\% \pm 9.9\%$ was in excreta indicating that most of the ingested chitin was lost in excreta rather than egested in pellets or digested.

A total of 49 pellets were collected from four screech owls. A total of $29.6\% \pm 9.1\%$ of ingested chitin was egested in pellets when 300 mg of chitin was fed per day (Table 1).

The percent of chitin egested in pellets relative to ingested chitin and apparent chitin digestibilities showed a strong negative correlation ($r = -0.76$, $P < 0.001$, Fig. 1) indicating that the more chitin egested in pellets, the less chitin was digested. When pellets were egested ($N = 14$) in kestrels, apparent chitin digestibilities were determined to be $19.5\% \pm 5.3\%$. When no pellets were egested ($N = 3$), digestibility was significantly higher at $28.9\% \pm 3.7\%$ ($P < 0.01$). This suggested that the lower GI tract may contribute in the digestion of chitin in kestrels. Kestrels possess a relatively long colon compared to their body size although the cecum is extremely small (Duke et al. 1997). If the contribution to chitin digestion is due to bacterial enzymes, their large colon might support possible

Table 1. Mean weights of chitin in pellets and percents of chitin egested, excreted and digested in American Kestrels and Eastern Screech Owls. Results are expressed as $\bar{x} \pm 1$ SD. The number in parentheses is the number of samples. The samples of chitin pellets were collected during the chitin feeding trials (American Kestrel) or the acclimation to a chitin diet (Eastern Screech Owl).

	AMERICAN KESTREL	EASTERN SCREECH OWL
Dry weight of chitin in chitin pellet (mg)	28.4 ± 14.3 (14)	88.9 ± 27.3 (49)
Percentage of chitin egested as pellet compared to total ingested chitin (%) ^a	23.8 ± 11.0 (14)	29.6 ± 9.1 (49)
Percentage of chitin excreted in excreta compared to total ingested chitin (%) ^b	59.2 ± 9.9 (17)*	
Apparent chitin digestibilities when chitin pellets were egested (%) ^c	19.5 ± 5.3 (14)**	
Apparent chitin digestibilities when no chitin pellets were egested (%) ^c	28.9 ± 3.7 (3)**	

^a 100(Chitin pellet/Chitin in).

^b 100(Chitin out – Chitin pellet)/Chitin in.

^c 100(Chitin in – Chitin out)/Chitin in.

Chitin pellet = total dry weight of chitin in chitin pellet.

Chitin in = total dry weight of ingested chitin.

Chitin out = total dry weight of excreted or egested chitin.

* Including three cases where no pellet was egested.

** Digestibilities when no pellets were egested were significantly higher than when pellets were egested ($P < 0.01$).

chitinolytic bacterial populations. Screech owls have a pair of relatively large ceca with the potential for bacterial fermentation indicating that enteric bacteria probably contribute to chitin digestion (Akaki 1997).

Chitin digestibilities determined using chitin powder are probably higher than digestibility of flakes or pieces of chitin obtained by eating insect prey. However, we felt that by feeding chitin with a uniform particle size and source our results

would be more consistent between experiments and species.

We found variation in the size of pellets (0–41.9% of ingested chitin by weight) egested by kestrels. We found similar variation in the pellets of one screech owl which egested 10.5–46.3% of ingested chitin in its pellets ($N = 36$), although the same amount of chitin was given to the bird every day. The causes of this variation are unknown.

Since pellets were collected under different conditions for kestrels and screech owls, it was impossible to compare the data obtained for the two species. Screech owls, however, appeared to egest chitin in pellets only when they were fed a relatively large amount of chitin (300 mg). In 80% of the feeding trials, kestrels egested chitin in pellets even when they were fed the 2% chitin diet (97.4–131.4 mg of chitin). Kestrels appear to be more sensitive to a small amount of undigested material remaining in the gizzard, but reasons are unknown.

The oral egestion of coarse chitin powder in pellets of kestrels and screech owls suggests that chitin is difficult to degrade and tends to be eliminated by raptors with other undigestible material such as hair and bones. Both species egested chitin in pellets 6–12 hr and 6–10 hr, respectively, after the feeding of chitin. In spite of their retention of chitin in their stomachs, chitin powder was still rec-

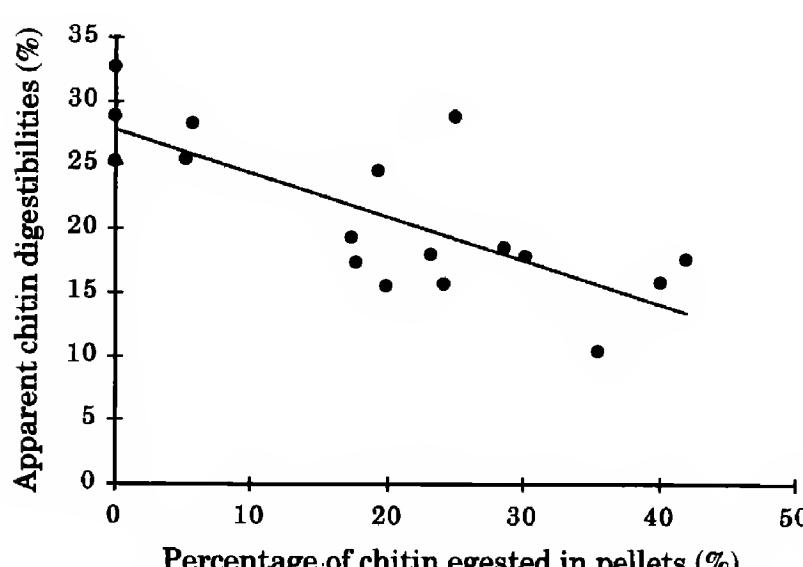


Figure 1. Relationship between apparent chitin digestibilities and percentage of chitin egested in pellets in three American Kestrels.

ognizable in the pellets and appeared macroscopically to be not significantly different from the original size indicating that the digestion of chitin in the stomach of these two species is very limited.

Although our results indicated that the lower GI tract contributed to chitin digestion in kestrels, chitin powder was still easily recognized in excreta indicating that chitin is difficult to digest even after exposure to digestive enzymes in the lower GI tract.

It has not been determined why raptors digest chitin despite the difficulty of its degradation. One possible reason is that chitinous exoskeletons of prey need to be digested to expose soft tissue to digestive enzymes (Gooday 1990). Since mechanical digestion in the stomachs of raptors appears to be limited due to a less muscular gizzard as compared to fowl (Duke 1986), more chemical digestion may be required. It is possible that chitin itself is utilized as an energy source by raptors, although the final products of chitin hydrolysis are difficult to absorb in the intestine (Capps et al. 1966, Crane 1968, Jackson et al. 1992). Since the absorption and metabolism of digested chitin by screech owls and kestrels has not been studied, further investigation is required in order to determine the value of chitin as an energy source for these species.

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AN INFRARED VIDEO CAMERA SYSTEM FOR MONITORING DIURNAL AND NOCTURNAL RAPTORS

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ABSTRACT.—A black and white, circuit-board video camera system with night vision was designed to monitor Mexican Spotted Owl (*Strix occidentalis lucida*) behavior. A 0.5-Lux infrared camera equipped with a 3.3 mm lens permitted vision up to 3 m in total darkness with the aid of six infrared light-emitting diodes (LEDs). To extend nighttime visibility at selected sites to approximately 6 m, we constructed a supplemental 9-LED infrared light source. Industrial-grade video recorders provided up to 24-hr coverage per VHS tape. Cameras averaged 6.9 m from nests (range 3.0–10.3 m). Mean camera installation time was 42 min (range 28–71 min). Between 25 April–3 July 1996, approximately 820 hr of video effort (76 hr for equipment assembly, 14 hr for camera placement, 230 hr for maintaining tapes and batteries, and 500 hr for subsequent video analysis) provided 2655 hr of usable video coverage (149 tapes) at 20 nest sites, a return ratio of nearly 3.2:1 hr of coverage for each hour invested. Comparable detail, quality, or quantity of behavioral data would not have been possible through direct observation. This video system could have a wide application in other raptor behavior studies, especially for determining the effects of human activities.

KEY WORDS: *behavior; diurnal activity; infrared photography; Mexican Spotted Owl; nocturnal activity; Strix occidentalis lucida; surveillance; video camera.*

Un sistema de video cámara infrarrojo para el monitoreo de aves rapaces diurnas y nocturnas

RESUMEN.—Un sistema de video cámara en blanco y negro con visión nocturna fué diseñado para el monitoreo del comportamiento de *Strix occidentalis lucida*. Una cámara de 0.5 Lux equipada con un lente de 3 mm permitió una visión de hasta 3 m en la obscuridad total con la ayuda de una luz infrarroja de seis diodos. Con el fin de extender la visibilidad nocturna a 6 m en sitios seleccionados, construimos una fuente de luz infrarroja suplementaria de 9 diodos. Con video grabadoras industriales cubrimos períodos de 24 horas en cintas de VHS. La distancia promedio de los nidos fue de 6.9 m (rango = 3.0–10.3 m). La media del tiempo de instalación de la cámara fue de 34 min (rango = 28–71 min). Entre el 25 de abril–3 de julio de 1996, 820 hr de video fueron registradas (76 hr para el ensamblaje del equipo, 14 hr para la ubicación de la cámara, 230 hr para el mantenimiento de cintas y baterías y 500 hr para el análisis de video) 2655 hr de cobertura de video (149 cintas) en 20 nidos, una tasa de retorno de cerca de 3.2:1 hr de cobertura por cada hora invertida. El detalle, la calidad o cantidad de datos de comportamiento no hubiera podido ser obtenida a través de observaciones directas. Este sistema de video puede tener una aplicación amplia en estudios de comportamiento de otras aves rapaces especialmente con el fin de determinar los efectos de actividades humanas.

[Traducción de César Márquez]

Collecting baseline behavioral information on animals from field observations is an important prerequisite to determining and mitigating the effects of human activities. To compare animal behavior between manipulated and nonmanipulated

sites or periods, it is often necessary to make simultaneous observations at more than one location and for extended periods of time. For studying owls, the ability to monitor nocturnal behavior is also critical. Recording wildlife activity with remotely operated or automatic cameras has a long history (Dodge and Snyder 1960, Osterberg 1962, Cowardin and Ashe 1965, Patton et al. 1972). Techniques include time-lapse, super-8 movie cameras (Grubb 1983), conventional video cameras (Nye

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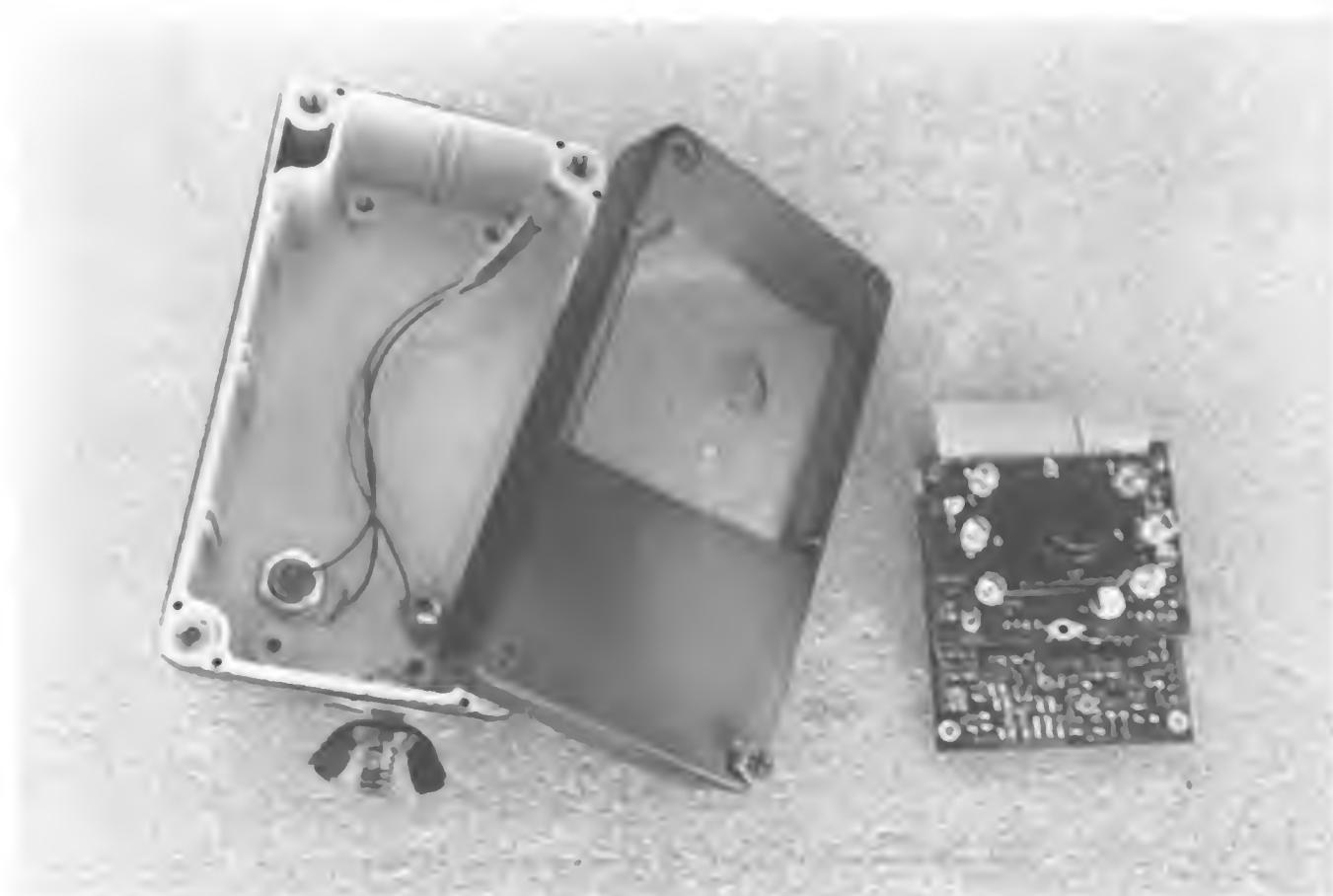


Figure 1. Miniature circuit-board video camera with weatherproof, plastic switch-box painted black (except for the lens and LED area) and wired for video and power connections.

1983, Kristan et al. 1996), miniature video-board cameras (Proudfoot 1996), 110 instamatic cameras (Jones and Raphael 1993), 35-mm infrared-aided cameras (Hernandez et al. 1997), and the most common approach, 35-mm, flash-aided photography (Major 1991, Kucera and Barrett 1993, Browder et al. 1995, Danielson et al. 1996).

During a recent study on the effects of helicopter and chain-saw noise on nesting Mexican Spotted Owls (*Strix occidentalis lucida*; Delaney et al. 1999a), we chose video surveillance as the primary means of recording owl behavior and responses to manipulations at nest sites because it did not require capturing or handling owls for radiotelemetry, could be operated remotely with minimal disturbance to the owls, was silent with no moving parts, provided both diurnal and nocturnal recording capability, and facilitated real time, behavioral analyses *a posteriori*. However, to meet the unique requirements of unobtrusively recording continuous behavior of this primarily nocturnal species, we had to design a camera system that was small and easily mounted, functional in both daylight and darkness, and sufficient for monitoring owl nesting activity and prey deliveries. This paper describes the design, construction, and deployment of this essentially noninvasive, infrared video camera sys-

tem for monitoring 24-hr activity at Mexican Spotted Owl nest sites.

METHODS

We used Marshall² black and white, charge-coupled device (CCD), circuit-board video cameras (Marshall Electronics, Culver City, CA U.S.A.; Fig. 1). The solid state, 12-volt, circuit-board cameras came equipped with 3.3-mm lenses, which we replaced in most cases with an optional 12.0-mm lens. A fully automatic electronic shutter compensated between bright daylight and nighttime conditions. The camera provided a minimum of 380 lines of resolution and with 0.5-Lux, permitted vision up to 3 m in total darkness with the aid of six infrared light-emitting diodes (LEDs; Figs. 1, 2A). To approximately double night vision capabilities (i.e., to monitor nests up to 6 m away), we designed supplemental infrared, 9-LED (Tandy Corp., Ft. Worth, TX U.S.A.), light sources on 5-cm (2-inch) diameter circuit boards mounted in PVC-pipe end caps sealed with plexiglass (Fig. 2B). Each of these lights was then attached to a 2-m piece of lightweight aluminum screen molding that facilitated independent mounting in camera trees closer to the nests under observation. Cameras were mounted in waterproof, heavy-gauge plastic switch-boxes with transparent covers (11.5 × 6.4 × 5.5 cm; Newark Electronics, Chicago, IL U.S.A.) which, ex-

² Use of trade names does not imply endorsement by the USDA Forest Service, Rocky Mountain Research Station, or Institute for Wildlife Studies to the exclusion of other potentially suitable products.

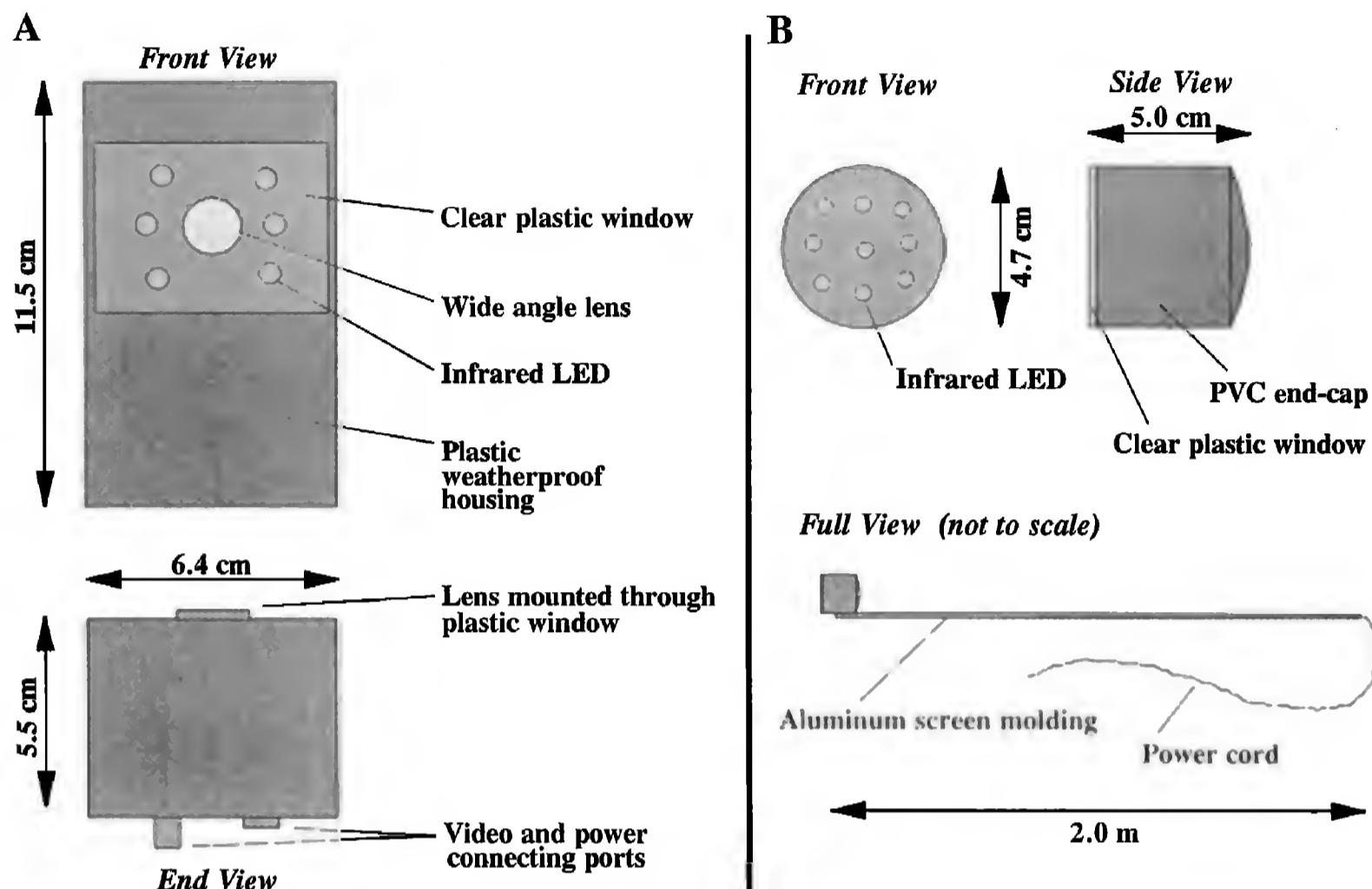


Figure 2. Schematics of (A) the black and white, circuit-board infrared video camera and (B) the supplemental, infrared light source used to extend night recording capability to ~ 6 m.

Table 1. Equipment and approximate costs for a night vision video surveillance system (based on 1996 prices associated with assembling 20 systems).

COMPONENT	APPROXIMATE COST (\$)
Video cassette recorder	745.00
Miniature video camera	240.00
DC monitor (\$110.00 per 4–5 systems) ^a	~25.00
Rechargeable batteries (\$55.00, 4 per system)	220.00
Battery charger (\$80.00 per 4–5 systems) ^a	~20.00
Coaxial and power cables, connectors, plugs	100.00
Protective bin	20.00
Tarpaulin and cord	30.00
Total	\$1400.00

^a Costs of DC monitors and battery chargers per system are proportionally reduced by the total number of systems deployed; we used 4 monitors (the same 10.5-cm DC monitors used to position the camera) and 4 chargers to operate 20 video systems.

cept for the lens and LED area, were painted black (Fig. 1). Two connecting ports were threaded into the protective housing for the power supply and the video signal. Cover plates were drilled to accommodate lens barrels, which when the outer portion was attached through the plate, supported the entire circuit board.

Panasonic Model AG-1070DC, industrial-grade VHS video recorders (Panasonic Corporation of America, Secaucus, NJ U.S.A.), connected to cameras via coaxial cable (RG-59), provided up to 24-hr coverage per tape. These 12-volt, DC-powered recorders were designed for law-enforcement surveillance applications. We obtained 24-hr coverage by recording approximately 5 frames per sec instead of the normal rate of 30 frames per sec. Cameras, supplemental lights, and video recorders were powered by two 12-volt, 33.0-amp-hr, Power-Sonic Model PS-12330, rechargeable batteries (Power Sonic, Redwood City, CA U.S.A.) connected in parallel because a 24-hr taping would draw a single battery below operational limits. These rugged, sealed "gel-cell" type batteries (weighing 11.3 kg each) reduced the risk of battery damage, and eliminated the potential for spillage during backpack transport. The total cost per system was about \$1400.00 (Table 1). Assembly time was approximately 4 hr per camera system.

Cameras were attached to tree branches or trunks with adjustable, jointed angle-brackets and screws (Fig. 3). Cameras were mounted at the same level or slightly above nest height in the nearest practical tree, which had to be large enough to climb to nest height and also far enough



Figure 3. Branch-mounted video camera showing jointed attachment bracket, adjustable in two planes. Power and video cables are attached through connectors on the rear of the unit (not visible in this view) and anchored to the supporting branch or tree trunk.

from the nest tree so as not to disturb incubating owls. A 15-m combination power line and coaxial cable (or down line) was attached to a 10.5-cm DC-powered monitor and battery (Fig. 4), so camera placement during installation could be directed from the base of the camera tree. A minimum of two persons was required for camera placement, a climber to position the camera and a person on the ground to check the video signal and direct placement. Once the camera was positioned, the down line was taped to the tree and the system was left inoperative for up to a week. This allowed owls to habituate to camera presence prior to experiencing the visible, dull red glow of the infrared LEDs once the system was powered. Visual sensitivity of Mexican Spotted Owls to infrared light is unknown; however, Konishi (1973) has shown that Barn Owls (*Tyto alba*) are not sensitive to such light. A supplemental light source, when needed, was extended toward the nest platform, then nailed, wired, or taped in place. Its power line was spliced to the camera's with quick-connects. To make the system operational, a

60-m trunk line was attached at the base of the tree (covered by 1.2-cm diameter hose for protection against rodents), permitting the power/recording station to be placed away and out of sight from the nest tree to minimize potential disturbance to the owls. We put the recorder, two batteries, and all connectors inside a weatherproof, rubberized storage bin (61 cm × 40 cm × 24 cm; Fig. 4) concealed under a camouflaged tarpaulin. Batteries and tapes were exchanged before and after each 24-hr recording period.

RESULTS

During 10 field days between 9 April–27 May 1996, cameras were placed at 20 nest sites (1–4 sites per d depending on travel time between sites) in the Sacramento Mountains of southcentral New Mexico. Mean placement time from arrival to departure from the nest site was 42 min (range =



Figure 4. Weatherproof, rubberized bin housing video recorder, batteries for powering entire system, and spare tapes, with a portable monitor used temporarily to check video image reception and quality.

28–71 min). Nest height averaged 15.3 m (range = 8.0–27.0 m) in 18 Douglas firs (*Pseudotsuga menziesii*) and one white fir (*Abies concolor*). One nest tree was not measured. Cameras averaged 6.9 m from nests (range = 3.0–10.3 m). Because effective night vision was limited to approximately 6 m, we were only able to collect nocturnal information at eight nests.

We mounted 18 cameras without flushing nesting owls. Two initial mounting efforts that caused a flush were immediately aborted, with the adults returning to their nests in <5 min. We were able to mount both cameras a week later with no further response. Aside from the two flushes in 22 mounting attempts, spotted owls appeared totally unaffected by the video systems once in place. Several owls that had done so previously, even continued to perch in camera trees. There was no nest abandonment, and 18 of the 20 nests were successful. Neither nest failure was related to video camera presence (Delaney et al. 1999a).

Between 25 April–3 July 1996, our surveillance systems yielded 149 tapes and 2655 hr of taped coverage. Approximately 230 field hr were required for changing tapes and batteries or about 1.5 hr per change. In addition, over 500 office hours were required to analyze the tapes for related spotted owl behaviors such as nest attentiveness, number

of prey deliveries, and number of female trips from the nest. A total of approximately 820 hr (including an additional 76 hr for equipment assembly and 14 hr for camera placement) were spent in obtaining the 2655 hr of usable video coverage, a return ratio of 3.2:1 of coverage for each hour invested.

DISCUSSION

We developed this infrared camera system to facilitate a study of helicopter noise effects on the threatened Mexican Spotted Owl (Delaney et al. 1999a). This conservative approach allowed us to observe natural behavior and spotted owl responses to experimental manipulations with minimal risk to the owls. In addition, video coverage permitted the quantification and differentiation of several subtle, nonflushing behaviors that not only facilitated and strengthened our assessment of disturbance, but also provided new insight into spotted owl nesting and foraging activities (Delaney et al. 1999b).

Previous raptor responses to camera installation ranged from no apparent effect (i.e., successful fledging; Enderson et al. 1973) to extreme effects such as nest abandonment (Cain 1985, W. Bowerman pers. comm.). Responses may be affected by installation time, season, and camera placement, as

well as by animal temperament and prior experience. Red-tailed Hawks (*Buteo jamaicensis*) and Northern Goshawks (*Accipiter gentilis*) have been disturbed by the mere human presence associated with research activity (Olendorff 1975, Kennedy and Stahlecker 1993). Although our cameras were carefully installed after spotted owls had initiated nesting, we strongly recommend installation prior to nesting activity and before breeding adults are present.

We would not have been able to collect the same level of detail, quality, or quantity of behavioral data through direct observation. Videotaping with the date and time on each frame provided a permanent record that could be accurately measured and reviewed for additional information. In addition, it provided uninterrupted 24-hr coverage and the capability of monitoring several nests simultaneously, thus minimizing confounding factors related to sample timing. To obtain comparable coverage via direct observation would have required 2–3 field assistants per site and tripled labor costs. Disruptive personnel shift changes and expensive night-vision equipment would also have been necessary.

Additional advantages of this camera system are that cameras are unmanned and provide 24-hr, real-time assessment of the frequency, duration, timing, and type of behaviors, as opposed to the more limited sampling regimes inherent in common forms of time-lapse or triggered photography. Infrared capability permits similar recording of nocturnal and diurnal activities without disruptive flashes. Remote placement allows observers to stay approximately 60 m from nests once cameras are installed, minimizing observer effects that might otherwise confound assessment of other human disturbances. The cameras are small, unobtrusive and quiet, and the cost per system is modest by comparison to other video systems.

We also experienced several difficulties or limitations in operating this system. Installing the 60-m cables for power and video and protecting the system from moisture, loose connections, rodent damage, and vandalism required that all cables be encased in garden hose, which had to be hidden from view and located away from any game trails to reduce possible damage. A combination of this infrared video camera system and the solar-powered transmitting system of Kristan et al. (1996) would eliminate these cumbersome cables and hoses. Night vision attenuated rapidly with distance

and was clearest when cameras and supplemental lights were <6 m from nest trees. Placing cameras 1–3 m above nests in the same tree would eliminate the supplemental light and maximize night recording clarity; however, this would have to be accomplished prior to occupancy to avoid disturbance or abandonment. Typical of any video system, direct sunlight and reflection off nearby foliage distorted contrast and limited visibility into shaded areas. These factors must be considered and minimized during camera placement.

Since our application, circuit-board video cameras have become less expensive while capabilities have increased to include color, sound, as well as small, factory-built weatherproof housings. In conclusion, miniature circuit-board video systems are a reliable, relatively unobtrusive, and effective tool for monitoring behavior of raptors and other wildlife in a wide variety of applications. Based on our experience, this technique can particularly benefit research designed to assess the effects of human activities and land management practices on threatened or endangered species.

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PREY OF BREEDING NORTHERN GOSHAWS IN WASHINGTON

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ABSTRACT.—We identified 936 prey from food remains and pellets collected at 82 Northern Goshawk (*Accipiter gentilis*) nest sites in Washington from 1986–96. Mammals and birds constituted half of the prey by frequency and biomass throughout Washington, although birds were more prevalent ($P = 0.050$) in the diet of goshawks nesting in the Olympic and Cascade mountains of western Washington (53%), than in the Cascades of eastern Washington (47%). Douglas' squirrels (*Tamiasciurus douglasii*), grouse (*Dendragapus obscurus* and *Bonasa umbellus*), and snowshoe hares (*Lepus americanus*) were jointly the most frequently represented prey on the west side (41%) and east side (54%). Grouse and snowshoe hares accounted for the overwhelming majority of prey biomass in these respective areas (76% and 80%). Relative to other Northern Goshawk populations, goshawks in Washington appeared to prey on species from a similar number of genera, but they had a smaller food-niche breadth and they took larger-sized birds primarily due to their high consumption of grouse. Northern Goshawks in western Washington took prey in more equal numbers than those on the east side. Potential bias from examination of prey remains when compared to pellets reinforced the need for inclusion of observations on prey deliveries at nests when determining the diet of nesting Northern Goshawks.

KEY WORDS: *Northern Goshawk; Accipiter gentilis; diet; food habits; grouse; hare; Washington.*

Presas del azor en reproducción en Washington

RESUMEN.—Identificamos 936 presas de restos de comida y egagrópilas recolectadas en 82 nidos de *Accipiter gentilis* en Washington desde 1986–96. Los mamíferos y las aves constituyeron la mitad de las presas por frecuencia y biomasa en Washington, aunque las aves prevalecieron ($P = 0.050$) en la dieta de las montañas Olympic y Cascade del oeste de Washington (53%), al contrario de las Cascade del este Washington (47%). *Tamiasciurus douglasii*, *Dendragapus obscurus*, *Bonasa umbellus* y *Lepus americanus* fueron en conjunto las presas mas representadas en el oeste (41%) y este (54%). *Dendragapus obscurus* y *Lepus americanus* representaron la mayoría de la biomasa de presas en estas areas respectivas (76% y 80%). Con relación a otras poblaciones de azores del norte, los azores de Washington aparentemente depredaron a especies de un número similar de géneros, pero tuvieron nichos de alimentación de menor tamaño y una media mayor en el peso de las aves, lo cual es el resultado del alto consumo de *Dendragapus obscurus* y *Bonasa umbellus*. Sin embargo, los azores del norte en el oeste de Washington tuvieron un uso mas equitativo de presas que los del este. El sesgo potencial del exámen de los restos de presas comparado con las egagrópilas refuerza la necesidad de incluir observaciones para la determinación de la dieta de los azores del norte en anidación.

[Traducción de César Márquez]

In the Pacific Northwest, the association of Northern Goshawks (*Accipiter gentilis*) with mature forests (Bull and Hohmann 1994, Hargis et al.

1994, Woodbridge and Detrich 1994) may be related to the structural characteristics of stands that optimize the availability of goshawk prey (Reynolds et al. 1992). Even where preferred prey are abundant, structural characteristics of habitat such as tree density and understory may reduce prey availability thereby affecting habitat selection and distribution of nests (Beier and Drennan 1997, DeStefano and McCloskey 1997).

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In Washington, nesting Northern Goshawks are distributed east and west of the Cascade Mountains, where there are different climates, forest communities and potentially different prey species and prey abundance. In western Washington, maritime influences at nest sites in the Olympic Mountains may further influence prey and diets of nesting Northern Goshawks. Diets in this area could be very different from that of goshawks nesting inland in the west Cascade Mountains. In the Coast Range of Oregon, for example, dense understory vegetation and high rainfall are believed to contribute to low populations of nesting goshawks due to their negative effects on prey availability (Reynolds and Wight 1978, DeStefano and McCloskey 1997). There is also the potential for dietary differences in Northern Goshawks nesting in managed stands in national forests and private timberland, where timber harvest may influence prey availability, and in national parks, where there is no timber harvest (Crocker-Bedford 1990).

Prey frequency, prey biomass, and food-niche breadth are commonly used to quantify raptor diets (Marti 1987). Methods of identifying raptor prey, including direct observation, examination of prey remains, and pellet examination provide data on diet, but each is subject to potential biases (Marti 1987). Here, we examine prey species identified in prey remains and pellets of nesting Northern Goshawks throughout Washington, with specific objectives to contrast prey frequency, biomass and food-niche breadth for populations of Northern Goshawks east and west of the Cascade Mountain crest; contrast major prey groups among sub-regions of these populations, and in areas potentially subject to timber harvest and those without harvest; identify differences in prey species or food-niche breadth peculiar to Washington Northern Goshawks relative to other areas in North America; and identify biases associated with identification of prey from remains or pellets.

STUDY AREA AND METHODS

Prey remains and pellets were collected at 38 Northern Goshawk nest sites in western Washington (16 in the Olympic Mountains, 22 in the Cascade Mountains) from 1986–96, and at 44 nest sites in the Cascades of eastern Washington (17 in the central Cascades, 27 in northern Cascades) from 1992–96 (Fig. 1). Prey and pellets were collected from nests, under nest trees, and at plucking posts. Most remains were collected incidentally during breeding surveys from the nestling stage through post-fledging, and nests were not sampled equally among years (65% sampled 1 yr, 24% sampled 2 yr, and 11%

sampled >2 yr). Most nest trees were in late successional forests and were located in national forests ($N = 58$), national parks ($N = 11$), private timberland ($N = 9$), and state land ($N = 4$). In ownerships other than national parks, landscapes surrounding nests and within nesting territories were potentially subject to forest management. The actual degree of timber harvest within these territories was unknown.

The climate in western Washington is characterized by mild, wet winters and warm, dry summers. Forests are predominantly Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Sitka spruce (*Picea sitchensis*) is present at a few lower elevation nest sites on the west side of the Olympic Peninsula. Forests in the Cascades of eastern Washington, a region with cool winters and hot, dry summers, are dominated by stands of Douglas-fir, ponderosa pine (*Pinus ponderosa*), and western hemlock.

For each collection of prey remains, we attempted to identify the minimum number of individuals represented to species level from pooled occurrences in food remains and pellets. Matched hair and feather samples from prey and pellets were considered to represent the same individual, whereas counts of pooled bones and flight feathers allowed for identification of >1 individual. When we found skeletal remains of snowshoe hares (*Lepus americanus*) and grouse (*Dendragapus obscurus* and *Bonasa umbellus*), we estimated the age of individuals through size comparisons with museum specimens and the degree of bone fusion at joints. Ages of these species were used to estimate their respective contributions to prey biomass. Solid remains (e.g., skeletal remains, beaks) were identified from museum specimens (University of Washington, Seattle, or University of Wisconsin, Madison) or identification keys (Olsen 1964, 1972). Fur and feathers were matched to museum specimens or descriptions in field guides (Peterson 1947, Burt and Grossenheider 1976). Arthropods were excluded from data analyses. Our suspicion was that many insects found in prey remains, particularly beetles and ants, were consumed indirectly when small mammals and grouse were eaten. Presence of ants was correlated ($r^2 = 0.18$, $P = 0.001$) with the occurrence of Douglas' squirrels (*Tamiasciurus douglasii*) and chipmunks (*Tamias* spp.) in prey remains, and stomach contents of three whole carcasses of Douglas' squirrels and chipmunks contained numerous beetle shell fragments. Several pellets contained insect fragments mixed with fir needles, seeds, and grouse remains.

We reported mammalian and avian prey by frequency and biomass. Biomass estimates were derived from average weights of species from Reynolds and Meslow (1984) and other published sources (Table 1). Weights were derived for juvenile and adult age classes of snowshoe hares and grouse. For prey for which we could estimate biomass (i.e., not including unidentified birds or mammals), we calculated the mean weight of avian prey (MWAP), mean weight of mammalian prey (MWMP) and mean weight of total prey (MWTP). Food-niche breadth was calculated for prey genera using the following equation (Levins 1968):

$$B = \frac{1}{\sum P_i^2}$$



Figure 1. Locations of Northern Goshawk nest sites in Washington State where prey were collected from 1986–96.

where P_i was the proportion of prey in each taxon. In order to compare food-niche breadth with other northern goshawk research, breadth was standardized (Reynolds and Meslow 1984) using:

$$B_s = (B - 1)/(n - 1)$$

where n = the total number of taxons. Values approaching 1 were indicative of relatively more equitable use of prey, with lower values indicative of narrower diet breadth.

We used chi-square contingency tests at the $P = 0.05$ significance level for frequency comparisons of prey species and classes by region (east side and west side, and four study areas) and collection type (prey remains or pellet), ages of major prey species (adult or juvenile) by region, and major prey species by forest management status (managed or unmanaged). Unidentified mammalian

and avian prey were excluded from analyses involving prey species, and prey with combined frequencies ≤ 1 were pooled into a miscellaneous species category.

RESULTS

We identified 936 prey at 82 Northern Goshawk nest sites. West side prey collections ($N = 38$ sites) accounted for 57% of identified prey, and east side collections ($N = 44$ sites) accounted for 43% of prey. An average of 11.0 ($SD = 10.5$, range = 1–53) individual prey items were identified per nest site. Prey remains were not identified beyond class for 11% of 465 mammalian remains and 17% of 471 avian remains. These remains typically consist-

Table 1. Northern Goshawk prey assessed from prey remains and pellets at 44 nest sites in the Olympic and Cascade mountains of western Washington, and at 38 nest sites in the Cascade mountains of eastern Washington from 1986–96.

SPECIES	COMMON NAME	WEIGHT (g) ^a	WESTERN WASHINGTON			EASTERN WASHINGTON		
			NO.	% ^b	% BIO- MASS ^c	NO.	% ^b	% BIO- MASS ^c
Mammals								
<i>Tamiasciurus douglasii</i>	Douglas' squirrel	201.2	80	15.1	9.6	78	19.2	10.0
<i>Lepus americanus</i>	snowshoe hare	^d	47	8.9	32.6	57	14.1	40.6
<i>Tamias</i> spp.	Unidentified chipmunk	80.5	31	5.8	1.5	26	6.4	1.3
Unidentified mammal	n/a		27	5.1	n/a	19	4.7	n/a
<i>Glaucomys sabrinus</i>	northern flying squirrel	167.0	28	5.3	2.8	12	3.0	1.3
<i>Clethrionomys gapperi</i>	red-backed vole	27.0 ^e	7	1.3	0.1	9	2.2	0.2
Unidentified vole		25.0	13	2.5	0.2	1	0.3	<0.1
<i>Peromyscus</i> spp.	Unidentified mouse	19.5 ^f	6	1.1	<0.1	6	1.5	<0.1
<i>Thomomys mazama</i>	Mazama pocket gopher	103.0 ^e	5	0.9	0.3	0	0.0	0.0
Unidentified small mammal	n/a		2	0.4	n/a	3	0.7	n/a
<i>Scapanus townsendii</i>	Townsend's mole	140.0 ^e	1	0.2	<0.1	1	0.3	<0.1
<i>Thomomys talpoides</i>	northern pocket gopher	104.0 ^e	0	0.0	0.0	2	0.5	0.1
<i>Ochotona princeps</i>	pika	146.5 ^e	1	0.2	<0.1	0	0.0	0.0
<i>Sorex cinereus</i>	masked shrew	4.5 ^e	1	0.2	<0.1	0	0.0	0.0
<i>Neotoma cinerea</i>	bushytail woodrat	396.0 ^e	0	0.0	0.0	1	0.3	0.3
<i>Martes americana</i>	marten	^g	0	0.0	n/a	1	0.3	n/a
Subtotal			249	47.0	47.1	216	53.5	53.8
Birds								
Unidentified grouse		^h	73	13.8	35.1	74	18.3	35.8
Unidentified bird		n/a	49	9.2	n/a	32	7.9	n/a
<i>Cyanocitta stelleri</i>	Steller's Jay	106.6	46	8.7	2.9	16	4.0	1.1
<i>Colaptes auratus</i>	Northern Flicker	148.8	26	4.9	2.3	23	5.7	2.2
<i>Ixoreus naevius</i>	Varied Thrush	79.3	25	4.7	1.2	4	1.0	0.2
<i>Turdus migratorius</i>	American Robin	81.2	18	3.4	0.9	1	0.3	<0.1
<i>Dendragapus obscurus</i>	Blue grouse	ⁱ	11	2.1	7.1	5	1.2	2.7
<i>Picoides villosus</i>	Hairy Woodpecker	48.3	3	0.6	<0.1	8	2.0	0.2
Unidentified woodpecker		165.2 ^j	7	1.3	0.7	3	0.7	0.3
<i>Perisoreus canadensis</i>	Gray Jay	89.4 ^k	9	1.7	0.5	0	0.0	0.0
Unidentified passerine		168.7 ^l	3	0.6	0.3	6	1.5	0.6
<i>Bonasa umbellus</i>	Ruffed Grouse	550.0 ^m	3	0.6	1.0	3	0.7	1.1
Varied Thrush or American Robin		80.0	1	0.2	<0.1	3	0.7	0.2
<i>Spinus pinus</i>	Pine Siskin	13.0	1	0.2	<0.1	3	0.7	<0.1
<i>Corvus</i> spp.	Northwestern or American Crow	460.0 ^f	2	0.4	0.6	1	0.3	0.3
Unidentified owl		259.0 ⁿ	0	0.0	0.0	3	0.7	0.5
<i>Bombycilla cedrorum</i>	Cedar Waxwing	33.5	1	0.2	<0.1	1	0.3	<0.1
<i>Glaucidium gnoma</i>	Northern Pygmy Owl	42.8 ^o	1	0.2	<0.1	0	0.0	0.0
<i>Junco hyemalis</i>	Dark-eyed Junco	17.6	1	0.2	<0.1	0	0.0	0.0
<i>Loxia leucoptera</i>	White-winged Crossbill	24.1 ^p	1	0.2	<0.1	0	0.0	0.0
<i>Sturnus vulgaris</i>	European Starling	74.5	1	0.2	<0.1	0	0.0	0.0
<i>Dryocopus pileatus</i>	Pileated Woodpecker	282.0	0	0.0	0.0	1	0.3	0.2
<i>Sphyrapicus varius</i>	Red-breasted Sapsucker	48.3 ^q	0	0.0	0.0	1	0.3	<0.1
<i>Anas platyrhynchos</i>	Mallard	1185.0 ^f	0	0.0	0.0	1	0.3	0.8
Subtotal			282	53.4	52.6	189	46.9	46.2

ed of hair samples and feather shafts, but no skeletal remains.

At least 13 species of mammals and 18 species of birds were identified in prey remains (Table 1). Douglas' squirrels, grouse (unidentified grouse, Blue Grouse [*Dendragapus obscurus*] and Ruffed Grouse [*Bonasa umbellus*]), and snowshoe hares were the most common prey species, and together accounted for 54% of all prey in eastern Washington and 41% in western Washington. They were also the most widely distributed prey, with Douglas' squirrels identified at 69% of the 82 nest sites statewide, grouse identified at 57% of nest sites, and snowshoe hares identified at 61% of all nest sites. Other species that accounted for $\geq 3\%$ of prey by frequency in both eastern and western Washington included chipmunks (*Tamias* spp.), northern flying squirrels (*Glaucomys sabrinus*), Steller's Jays (*Cyanocitta stelleri*) and Northern Flickers (*Colaptes auratus*). Passerines accounted for 28% of west side prey and 18% of east side prey.

Mammals and birds composed equal proportions (50%) of goshawk prey throughout Washington by frequency. However, proportions of mammals and birds in prey remains differed between western and eastern Washington ($\chi^2 = 3.81$, df = 1, $P = 0.050$). Birds were more prevalent than mammals in prey remains of west side goshawks (53% vs. 47%), while mammals more prevalent than birds on the east side (53% vs. 47%). Relative

to other birds, proportions of grouse, Steller's Jays, Varied Thrush (*Ixoreus naevius*), American Robins (*Turdus migratorius*), and Gray Jays (*Perisoreus canadensis*) were greater in west side than east side avian remains ($\chi^2 = 38.89$, df = 5, $P = 0.001$). Conversely, relative to other mammals combined, proportions of Douglas' squirrels and snowshoe hares in east side remains were greater than in western Washington ($\chi^2 = 6.96$, df = 2, $P = 0.031$).

Mammals and birds accounted for similar proportions of prey biomass throughout Washington (51% and 49%, respectively). While Douglas' squirrels were the most prevalent species in prey remains, they accounted for only 10% of prey biomass on both east and west sides (Table 1). Snowshoe hares and combined grouse species were the most important to overall biomass. These taxons accounted for 80% of all prey biomass in eastern Washington, and 76% of all biomass in western Washington. Adult specimens accounted for much of the biomass; adult snowshoe hares composed 87% of 67 hares that were aged, and adult grouse composed 75% of 113 grouse remains that were aged. There was no difference in age of captured snowshoe hares ($P = 0.458$) or grouse ($P = 0.410$) between eastern and western Washington. Other prey species contributed $<3\%$ of overall biomass throughout Washington (Table 1).

Mean weight of mammalian ($N = 399$), avian ($N = 390$) and total prey was 411, 415, and 413 g,

←

^a Weight of individual prey item used in biomass estimation. From Reynolds and Meslow (1984) unless noted otherwise.

^b Percent of prey in overall diet.

^c Percent of prey biomass to overall biomass.

^d Weight of juvenile (150 g) and adult *L. americanus* (1500 g) from Forsman et al. (1984); mean weight of adult and juvenile used to estimate weight of unaged specimens. Remains included 27 adults, 3 juveniles and 16 unaged specimens.

^e Burt and Grossenheider (1976).

^f Steenhof (1983).

^g Mass for this prey not used in estimate of biomass due to the inherent bias; guard hairs found in pellets likely from a scavenged carcass.

^h Average weight of adult (1053 g) and juvenile (909 g) *D. obscurus* (Zwickel et al. 1966) and adult (575 g) and juvenile (550 g) *B. umbellus* (Bump et al. 1947); mean weight of adults and juveniles used to estimate weight of unaged specimens. Remains included 37 adults, 9 juveniles and 30 unaged specimens.

ⁱ Average weight of adult and juvenile *D. obscurus* (Zwickel et al. 1966); mean weight of adult and juvenile used to estimate weight of unaged specimens. Remains included 4 adults, 1 juvenile and 7 unaged specimens.

^j Average weight of *P. villosus* and *D. pileatus*.

^k Average weight of unidentified jay from Reynolds and Meslow (1984).

^l Average weight of passerines identified to species.

^m Average weight of juvenile *B. umbellus* (Bump et al. 1947). Remains were of 1 juvenile.

ⁿ Used weight of medium-sized owl (*Asio otus*) from Karalus and Eckert (1974).

^o Karalus and Eckert (1974).

^p Average weight of White-crowned Sparrow (*Zonotrichia leucophrys*) from Reynolds and Meslow (1984).

^q Used weight of *P. villosus* from Reynolds and Meslow (1984).

respectively. The standardized food-niche breadth (FNB) was 0.27, based on frequencies of prey among 20 genera. However, goshawks in western Washington had a more equitable use of prey (FNB = 0.44, 18 genera) than those in eastern Washington (FNB = 0.31, 16 genera).

Proportions of mammals and birds in the diet were different ($\chi^2 = 17.67$, df = 3, $P = 0.001$) among prey of goshawks nesting in the Olympic Range, western Cascade Range, the central/southern east Cascades, and northern Cascades in eastern Washington ($N = 16, 22, 27$, and 17 territories, respectively). Goshawks in the central and southern Cascades of eastern Washington ate the highest proportion of mammals (57%), with fewer mammals eaten in the Olympic Range (54%), northern Cascades in eastern Washington (44%), and west Cascade Range (41%). Proportions of Douglas' squirrels in prey remains differed ($\chi^2 = 14.79$, df = 3, $P = 0.002$) among goshawks in the central and southern region of the east Cascades (22%), Olympic Range (20%), northern Cascades in eastern Washington (15%), and west Cascades (11%). Proportions of snowshoe hares also differed ($\chi^2 = 11.73$, df = 3, $P = 0.008$) in the central and southern region of the east Cascades (16%), Olympic Range (10%), northern Cascades in eastern Washington (10%), and west Cascades (7%). Proportions of grouse were different ($\chi^2 = 22.43$, df = 3, $P = 0.001$) in the northern Cascades in eastern Washington (32%), west Cascades (20%), central and southern region of the east Cascades (17%), and Olympic Range (12%).

We found no difference ($P = 0.853$) among frequencies of Douglas' squirrels, snowshoe hares and grouse relative to each other on land ownerships with potential timber harvest (i.e., national forest, state, and private land) and without harvest (i.e., national park).

We collected pellets 17% less often ($\chi^2 = 5.34$, df = 1, $P = 0.021$) when sampling nests on the west side ($N = 47$ visits) compared to the east side ($N = 76$ visits). We suspected that some skeletal remains on the west side were misclassified as coming from prey remains rather than pellets due to the rapid breakdown of pellets in the moist climate. Twenty-eight percent more birds than mammals were identified in prey remains when compared to pellets ($\chi^2 = 81.59$, df = 1, $P = 0.001$). Remains of snowshoe hares were 24% more prevalent among prey than pellets when compared to all mammals of smaller size ($\chi^2 = 19.81$, df = 1, P

= 0.001). Remains of grouse were 15% more prevalent among prey than pellets when compared to other birds ($\chi^2 = 15.82$, df = 1, $P = 0.001$).

DISCUSSION

Raptor diets are most accurately described through the combination of observations of prey deliveries at nests and prey collections (Marti 1987). We identified biases associated with the identification of only Northern Goshawk prey remains that overemphasized snowshoe hares and grouse, and believe that by including pellets in the analysis a more complete representation of the actual diet results, particularly in regard to the importance of small mammals. In western Washington, the predominance of collected prey remains compared to pellets may have partly accounted for the greater occurrence of avian prey, particularly grouse, on the west side. We were unable to identify biases that may have resulted from a lack of observations at nests. This may have underestimated the consumption of arthropods and reptiles as was found for *Accipiters* in Oregon (Reynolds and Meslow 1984), and overemphasized avian prey in the diet as determined in several studies (Ziesemer 1981, Reynolds and Meslow 1984, Boal and Mannan 1994). We concluded that most arthropods were eaten by goshawks incidental to the consumption of other prey. Although we identified no reptiles as prey, reptiles, notably garter snakes (*Thamnophis* spp.), were common in all forests we studied throughout Washington (K. McCallister pers. comm.). Other studies have not identified these same biases from prey sampling methodologies. For example, prey and pellet analysis of nesting Northern Goshawks in northeast Spain over-represented *Leporids*, and under-represented thrushes and small birds (Mañosa 1994). The rank of prey taxons assessed from prey remains, pellets and observations did not differ for breeding goshawks in New Mexico (Kennedy 1991). These differences reemphasize the importance of observations of prey deliveries for determining diets of specific populations of nesting goshawks.

Variation in the seasonal and annual timing of prey collections among nest sites introduced other potential biases in diet assessment. Seasonal changes in diet composition of Northern Goshawks may include a shift to fledgling passerines and increased diet diversity as nesting progresses (Squires and Reynolds 1997). Thus, prey constitution may change from the nestling to fledgling pe-

riods of the nesting phenology. Our geographical comparisons of Northern Goshawk prey in Washington were based on irregular prey collections over the 10-yr period and at different times of the nesting period; westside prey were collected throughout the entire 10-yr period, whereas east-side prey were collected over a 5-yr period. These collections were a composite of several studies, and each nest site was not sampled equally. It was not known how, or if, cyclic changes of major prey species throughout the state may have biased our analyses because we did not monitor their spatial or temporal variability. In the northern boreal forest, snowshoe hare and Ruffed Grouse undergo region-wide cyclic population fluctuations approximately every 10 yr (Keith and Rusch 1986, Doyle and Smith 1994, Hik 1994). Populations of other potential prey, particularly Douglas' squirrels, may also be subject to periodic cycles depending on the annual production of cones by conifer forests (Buchanan et al. 1990). However, Douglas' squirrels accounted for little biomass relative to other frequently eaten prey of goshawks in Washington suggesting a lesser importance of this species in the diet overall. Reduced hare numbers in southwest Yukon resulted in dietary shifts to smaller mammalian prey and increased avian consumption (Doyle and Smith 1994). A sudden decline in European hare (*Oryctolagus cuniculus*) in northeastern Spain resulted in a reduction in rabbit consumption by nesting goshawks and increased predation on Red-legged Partridge (*Alectoris rufa*) (Mañosa 1994). Consequently, if cyclic population phenomena are similar for hare and grouse in Washington, our regional comparison of prey could, at best, be interpreted to reflect actual differences in statewide prey selection; or, at worst, to be merely the identification of prey species eaten by breeding goshawks in eastern and western Washington.

The same prey species eaten by goshawks in eastern and western Washington accounted for the greatest biomass and frequency of prey in these areas (i.e., snowshoe hares, grouse, and to a lesser degree, Douglas' squirrels, chipmunks, Steller's Jays, and Northern Flickers). These same species have been found to be important prey throughout the goshawk's North American range (Reynolds et al. 1992, Squires and Reynolds 1997). Compared to goshawk diets in other Pacific Coast states, the most pronounced latitudinal differences appear to be the prominence of grouse in diets of Northern Goshawks in Washington relative to southern pop-

ulations in California (Bloom et al. 1986, Woodbridge et al. 1988) and a greater consumption of snowshoe hares relative to northern populations in southeast Alaska where hares are evidently uncommon (Titus et al. 1994). In California, primary prey species were Douglas' squirrels, Steller's Jays, and Northern Flickers; lagomorphs and sciurids comprise 66% of the total biomass (Bloom et al. 1986). In the southern Cascades of northern California, Steller's Jays and four species of woodpeckers are the principal birds taken and sciurids account for over half of the total biomass (Woodbridge et al. 1988). In Washington, we found grouse accounted for 42% of total biomass and lagomorphs and sciurids composed an additional 46% of total biomass. Even assuming unidentified grouse were the smallest juvenile grouse and unaged hares were all smaller juveniles, these taxons still accounted for 42% and 44% of total biomass, respectively. In southeast Alaska, goshawks eat high numbers of Blue Grouse which were identified at 73% of 25 nest sites, but snowshoe hare were found at only one nest (Titus et al. 1994). Additionally, Steller's Jays, Varied Thrush, and red squirrels (*Tamiasciurus hudsonicus*) have been found at >47% of the southeast Alaskan territories. Comparatively few small mammals are available as prey, which may limit populations (Titus et al. 1994). Queen Charlotte Goshawks on Vancouver Island eat species similar to those eaten by goshawks in Washington including Steller's Jays, Varied Thrush, and Northwestern Crows (*Corvus caurinus*) (Beebe 1974). Shorebirds and seabirds are also common prey, but we did not record them as prey in Washington, most likely because no nests in our study were located near seacoasts.

Even though regional and study area prey class proportions in Washington were statistically different (e.g., regional variation of 46–54%, study area variation of 41–59%), dietary class proportions were more similar to goshawk diets in New Mexico, Arizona and Oregon than to diets in New Jersey and California (Table 2). Goshawks in New Jersey and California eat 10–15% fewer mammals and 10–15% more birds compared to goshawks in Washington. More recent prey collections at goshawk nests in three different areas of eastern Oregon found frequencies of mammalian prey varied from 38–66% (Bull and Hohmann 1994, DeStefano et al. 1994). These results indicate that there can be as much variation in proportions of major prey species and classes of prey between

Table 2. Comparative food-niche breadths (standardized) and prey class ratios of Northern Goshawks in North America. Diet parameters are based on prey remains and pellets collected at nests unless indicated otherwise.

LOCATION	NESTS	MAMMAL : BIRD RATIO	FOOD-NICHE BREADTH (NUMBER GENERA)		SOURCE
New Jersey	16	30:70	0.26 (22)		Bosakowski et al. (1992)
Arizona	20	53:47	0.29 (18)		Boal and Mannan (1994) ^a
Eastern Washington	44	53:47	0.31 (16)		this study
New Mexico	8	49:51	0.36 (22)		Kennedy (1991) ^{b,c}
California	114	32:68	0.41 (21)		Bloom et al. (1986) ^{a,c}
Western Washington	38	47:53	0.44 (18)		this study
Oregon	59	45:55	0.45 (30)		Reynolds and Meslow (1984) ^c

^a Analysis of prey remains.

^b Pellet analysis.

^c Standardized food-niche breadth calculated by Boal and Mannan (1994).

study areas separated by <100 km, as there can be in nests separated by several hundred kilometers. Dietary proportions of mammals and birds are reflective of the abundance and availability of potential prey species throughout the range of the Northern Goshawk (Reynolds et al. 1992), suggesting there was considerable variation in local abundance or availability of key prey in Washington. We did not find a relationship in the occurrence of major prey types among managed and unmanaged forests, which we hypothesized might be a factor influencing local prey abundance or availability.

Relative to five other breeding populations throughout the U.S., goshawks nesting in eastern Washington had a low food-niche breadth while those in western Washington had a high food-niche breadth. While similar species were eaten, east side goshawks tended to eat large, cyclic prey such as hares and grouse more frequently. The high consumption of grouse throughout the state resulted in a mean avian prey weight (415 g) that was higher than that reported in New Jersey (332 g) and Connecticut (337 g) (Bosakowski et al. 1992), and Oregon (195 g) (Reynolds and Meslow 1984). The mean weight of mammalian prey (411 g) in Washington was more similar to the range of the average mammalian prey in these same studies (423–445 g). The variety of species we identified as prey suggested that nest occupancy and productivity of goshawks in Washington is not dependent on cyclic fluctuations in the populations of grouse and hare alone, although east side goshawks were more specialized feeders during this study.

While the species is an opportunistic feeder (Doyle and Smith 1994), without a variety of prey

species to buffer the effects of specialized feeding, goshawk productivity may mirror the changes in cyclic prey populations (Reynolds et al. 1992, Doyle and Smith 1994). Monitoring temporal changes in hare and grouse populations to assess their cyclic tendencies, and simultaneous collection of prey at the same goshawk nest sites over several years, both in eastern and western Washington, would provide an informative contrast as to the importance of cyclic prey to nest site occupancy and productivity.

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FOOD HABITS OF THE GREAT HORNED OWL (*BUBO VIRGINIANUS*) IN A PATAGONIAN STEPPE IN ARGENTINA

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ABSTRACT.—We studied seasonal variation in the diet of the Great Horned Owl (*Bubo virginianus*) through pellet analysis. Pellets were collected every month during 1995–96 from a steppe area in northwest Patagonia, Argentina. We identified 1216 prey items in 522 pellets. Rodents accounted for 98.5% of the diet while the remainder consisted of a variety of birds and insects. Rodents most frequently found in pellets were *Eligmodontia morgani*, *Abrothrix longipilis*, *A. xanthorhinus*, *Oligoryzomys longicaudatus*, *Reithrodon auritus*, and *Ctenomys haigi*. In terms of biomass, the most important species were *R. auritus*, *A. longipilis*, *C. haigi*, and *E. morgani*. Food-niche breadth was greatest in winter. Within the study area, the Great Horned Owl should be considered to be a rodent specialist all year round.

KEY WORDS: *Great Horned Owl*; *Bubo virginianus*; *diet*; *rodents*; *Patagonia*.

Hábitos alimentarios del *Bubo virginianus* en un área esteparia del noroeste de la Patagonia Argentina

RESUMEN.—Se estudió estacionalmente la dieta de *Bubo virginianus* mediante el análisis de egagrópilas recolectadas mensualmente durante los años 1995 y 1996, en un área esteparia del noroeste de la Patagonia Argentina. Fueron analizadas 522 egagrópilas que contenían 1216 presas. El 98.5% de las presas eran roedores, mientras que el 1.5% restante eran principalmente aves e insectos. Entre los roedores consumidos se encontraron en mayor número ejemplares de *Eligmodontia morgani*, *Abrothrix longipilis*, *A. xanthorhinus*, *Oligoryzomys longicaudatus*, *Reithrodon auritus* y *Ctenomys haigi*. En términos de biomasa, las mayores contribuciones corresponden a *R. auritus*, *A. longipilis*, *C. haigi* y *E. morgani*. La amplitud trófica alcanza el valor máximo en el invierno. En el área estudiada *B. virginianus* puede considerarse un especialista en roedores durante todo el año.

[Traducción de Autores]

The Great Horned Owl (*Bubo virginianus*) is distributed widely throughout the Americas and it lives in a variety of different habitats (Burton 1992). Its food habits have been studied at many different sites in North America. In South America, several quantitative studies have been carried out in Chile (Jaksic et al. 1978, Yáñez et al. 1978, Jaksic and Yáñez 1980, Jaksic and Martí 1984, Jaksic et al. 1986, Iriarte et al. 1990) and Argentina (Donázar et al. 1997). Martí et al. (1983) reviewed studies of the owl's diet in North and South America. Most of these studies reported Great Horned Owls mainly preying on rodents and lagomorphs, although there were regional, seasonal, yearly and long-term differences in diet.

Our study analyzed the food habits of the Great Horned Owl in a steppe area in northwest Patagonia, Argentina, and described the seasonal

changes in diet composition and food-niche breadth over two years (1995–96).

STUDY AREA AND METHODS

Our study was conducted in northwest Patagonia, east of the city of Bariloche, Argentina (41°08'–41°08'45"S, 71°12'–71°13'20"W). The study site was located in a steppe area of the transition zone between the subantarctic forests and the Patagonian steppe. The area is dominated by bunchgrasses such as *Stipa speciosa* and *Acaena splendens* and scattered bushes (*Senecio filaginoides*, *Baccharis linearis*, *Colletia hystrrix* and the exotic species *Rosa rubiginosa*). A road lined by exotic conifers (*Pinus* spp. and *Cupressus* spp.) ran through the area. These trees provide roosts for the Great Horned Owl.

The small mammal community in the area has been studied by Guthmann (1996) and Guthmann et al. (1997). According to them, the fauna consists of representatives of forest and steppe species dominated by *Eligmodontia morgani*, *Reithrodon auritus* and *Abrothrix xanthorhinus*, which are typical of semiarid steppe. *A. longipilis*

inhabits areas of dense forest to bushy steppe, and *Oligoryzomys longicaudatus* is abundant in brush areas and the edges of forests (Pearson 1995). Smaller numbers of *Loxodontomys micropus* inhabit humid or mesic brushy habitats, and *Ctenomys haigi* inhabits open areas with sandy soils (Pearson 1995). There were so far no records of other nocturnal raptor species within the study site, although Barn Owls (*Tyto alba*) were probably in the area.

Owl roosts were located by observing areas of white-wash or recording places where pellets were found. Pellets were collected monthly from February 1995–November 1996 at six known roost sites. Pellets were air dried and their length and width was measured with an electronic caliper to the nearest 0.01 mm. The pellets were dissected using standard techniques (Yalden 1990). Variations in measurements were related to the number of prey contained in the pellets by means of a one-way ANOVA. Prey biomass was calculated only for rodents. Mass estimates for each prey taxon were either determined from individuals captured in the study area or taken from literature.

Prey were identified to the finest possible taxonomic level. Mammalian prey were identified and quantified on the basis of skulls and dentary pairs using reference collections and keys (Pearson 1995). Insects were quantified by counting head capsules and mandibles. For other prey items, reference collections were used and they were quantified by assuming minimum number of individuals (e.g., feathers or scales of a given species were deemed to represent only one individual). Diet composition was compared between seasons and years with chi-square and G tests.

The contribution of each rodent species to the biomass of the owls' diet was calculated by multiplying mean body mass of individuals by number of individuals in the pellets. Values were expressed as a percentage of total rodent biomass consumed.

Food-niche breadth (FNB) was estimated using Levins' (1968) index: $FNB = 1/(\sum pi^2)$, where pi is the proportion of prey taxon I in the diet. A standardized-niche breadth value (FNB_{st}) was calculated, which ranged from 0 to 1: $FNB_{st} = (FNB - 1)/(n - 1)$, where n is the total number of prey categories (Colwell and Futuyma 1971). Evenness of prey numbers was measured using the Shannon-Wiener function J' (Krebs 1989): $J' = H'/\log n$, where H' is the Shannon-Wiener formula and n is the total number of prey categories.

RESULTS

A total of 1216 prey items was identified from 522 pellets. The mean number of prey/pellet was 2.3 (SD = 1.1; range = 1–7). Pellet measurements ranged from 2.3–8.8 cm long ($\bar{x} = 4.5$; SD = 1.1; $N = 516$) and from 1.4–4.3 cm wide ($\bar{x} = 2.7$; SD = 0.4; $N = 516$). Significant differences ($P < 0.05$) were found for both length ($F = 17.365$, df = 4,507) and width ($F = 20.365$, df = 4,506) and they appeared to be related to the number of prey in each pellet.

Rodents accounted for 98.5% of the prey (Table

1). The remaining 1.5% consisted of birds, insects, one lizard, and one lagomorph (a young *Lepus* about 0–6 months old according to cranial sutures described by González [1993]). We found one individual each of the following birds in the diet: *Tachycineta leucopyga*, *Troglodytes aedon*, *Sicalis luteola*, *Zonotrichia capensis*, *Anthus sp.*, and one unidentified Furnariidae. Insects that could be identified were Coleopterans (one of them Scarabaeidae) and Lepidopterans.

Great Horned Owls preyed mainly on *Eligmodontia morgani* over both years of the study, followed by *Abrothrix longipilis*, *A. xanthorhinus*, *Oligoryzomys longicaudatus*, *Reithrodon auritus*, *Ctenomys haigi*, and *Loxodontomys micropus*. The number of rodents consumed varied seasonally and was lower during winter. There were significant differences between the number of prey of different species eaten in 1995 and 1996 ($\chi^2 = 14$, df = 6, $P < 0.05$). The greatest difference between the two years was the lower than expected consumption of *L. micropus* and *O. longicaudatus* in 1996. There were no significant differences in the number of different species consumed between winters ($\chi^2 = 10.01$, df = 6, $P < 0.05$), but consumption of prey did differ significantly between summers ($\chi^2 = 35.93$, df = 6, $P < 0.05$), autumns ($G = 29.64$, df = 6, $P < 0.05$) and springs ($\chi^2 = 33.74$, df = 6, $P < 0.05$).

The mean weight of rodent prey ranged from 15.3 g for *A. xanthorhinus* to 146.2 g for *C. haigi* (Table 2). *R. auritus*, *C. haigi* and *E. morgani* contributed most to the prey biomass and all three were consumed in a greater proportion in 1996 than in 1995. In the pellets collected during 1995, the proportion of *R. auritus* in the diet fell considerably in spring, while that of *A. longipilis* and *C. haigi* rose.

Food-niche breadth was greatest in winter and smallest in spring during both 1995 and 1996. Although the number of prey types was highest in spring, evenness was lower than in winter (Table 1). The standardized-niche breadth calculated for the two years ($FNB_{st} = 0.202$) was slightly lower than for breeding seasons (spring and summer) for both years ($FNB_{st} = 0.218$, $N = 4$).

DISCUSSION

Because of their small size, Great Horned Owls that occur in southern South America have been placed in their own subspecies (*B. v. magellanicus*, Traylor 1958) and it has even been suggested that they in fact belong to their own species (*Bubo ma-*

Table 1. Seasonal diet of Great Horned Owls in northwestern Patagonia, Argentina. *N* = number of prey in each taxon; % calculated over the total number of prey for each.

PREY TYPE	1995							
	SUMMER		AUTUMN		WINTER		SPRING	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
MAMMALS								
Rodents								
Muridae								
<i>Abrothrix longipilis</i>	7	5.8	10	11.1	40	14.5	97	35.9
<i>Abrothrix xanthorhinus</i>	7	5.8	1	1.1	32	11.6	12	4.4
<i>Eligodontia morgani</i>	39	32.5	19	21.1	70	25.5	58	21.5
<i>Loxodontomys micropus</i>	2	1.7	10	11.1	12	4.4	10	3.7
<i>Chelemys macrouryx</i>	—	—	—	—	—	—	1	0.4
<i>Reithrodont auritus</i>	25	20.8	24	26.7	60	21.8	9	3.3
<i>Oligoryzomys</i>	27	22.5	18	20.0	25	9.1	43	15.9
<i>Geoxus valdivianus</i>	—	—	—	—	—	—	—	—
<i>Irenomys tarsalis</i>	—	—	—	—	—	—	—	—
Unidentified	7	5.8	5	5.6	30	10.9	21	7.8
Ctenomyidae								
<i>Ctenomys haigi</i>	3	2.5	4	4.4	6	2.2	15	5.6
Lagomorphs								
<i>Lepus europaeus</i>	—	—	—	—	—	—	—	0.0
BIRDS								
Passeriformes	1	0.8	—	—	—	—	2	0.8
REPTILES								
<i>Liolaemus</i> sp.	—	—	—	—	—	—	—	—
INSECTS								
—	2	1.7	—	—	—	—	2	0.7
SPIDERS								
—	—	—	—	—	—	—	—	—
Total prey	120		90		275		270	
Total pellets	42		37		130		114	
FNBst	0.446		0.667		0.672		0.308	
J'	0.773		0.880		0.892		0.700	

FNBst = food-niche breadth measured with standardized Levins' index (see text for explanations).

J' = preys number evenness by Shannon-Wiener function.

gellanicus, König et al. 1996). Owing to their small size, the average length and width of their pellets are among the smallest reported for Great Horned Owls. Yáñez et al. (1978) studied Great Horned Owl pellets from two regions in Chile, and found that those that contained remains of rodents were significantly wider than those containing arthropods. We could not verify this relationship in our study because the pellets contained almost exclusively rodents. Nevertheless, we did find that, in terms of the number of prey contained in pellets, there was less variation in pellet width than length. This could have been related to the fact that the

gape of the owls limited the size of the pellets they regurgitated. The low correlation between biomass and size of pellets could be a consequence of estimating biomass as average prey weight, without considering that the predator might select the size of its prey.

Studies in Chile (Yáñez et al. 1978, Jaksic et al. 1986, Iriarte et al. 1990) have found that, in some seasons, Great Horned Owls eat birds, insects, arachnids, and lagomorphs (up to 17% in Torres del Paine National Park [Iriarte et al. 1990]). In our study, these prey made up a negligible part of the diet. Near Junín de los Andes, Argentina, Don-

Table 1. Extended.

1996											
SUMMER		AUTUMN		WINTER		SPRING		TOTAL			
N	%	N	%	N	%	N	%	N	%		
49	25.0	12	14.5	11	15.7	31	27.4	257	49.2		
25	12.8	3	3.6	11	15.7	7	6.2	98	18.8		
59	30.1	31	37.2	16	22.9	23	20.4	315	60.3		
3	1.5	—	—	—	—	4	3.5	41	7.9		
—	—	—	—	—	—	—	—	1	0.2		
19	9.7	6	7.2	10	14.3	21	18.6	174	33.3		
17	8.7	9	10.8	7	10.0	7	6.2	153	29.3		
—	—	1	1.2	—	—	—	—	1	0.2		
—	—	—	—	—	—	1	0.9	1	0.2		
12	6.1	16	19.3	8	11.4	10	8.8	109	20.9		
6	3.1	5	6.0	5	7.1	3	2.7	47	9.0		
—	—	—	—	1	1.4	—	—	1	0.2		
2	1	—	—	1	1.4	—	—	6	1.2		
—	—	—	—	—	—	1	0.9	1	0.2		
2	1.0	—	—	—	—	4	3.6	10	2.0		
—	—	—	—	—	—	1	0.9	1	0.2		
196		83		70		113		1216			
73		33		39		54		522			
0.394		0.429		0.672		0.376		0.202			
0.746		0.794		0.885		0.764		0.597			

ázar et al. (1997) found the diet of Great Horned Owls consisted of 11.9% *Lepus europaeus* and 27.3% arthropods but, in terms of biomass, the two main prey items (55.2% of total prey) were juveniles of introduced lagomorphs (*L. europaeus* and *Oryctolagus cuniculus*).

Lagomorphs are considered to be the best prey for horned owls because their large body mass best suits the daily energy requirements of owls (Donázar et al. 1989). In our study, the number of lagomorphs in the diet was remarkably low despite the apparent abundance of *L. europaeus* in the area (7–12 individuals/ha, Novaro et al. 1992). According to Jaksic (1986), this situation is common for small

mammal predation in shrublands and grasslands of southern South America, with predators hunting mainly the most abundant native rodents, sometimes "ignoring" dense populations of introduced lagomorphs.

The proportion of lagomorphs we found in the diet did not support the generalization by Donázar et al. (1997) that lagomorphs represent 15% by number of the diet of Great Horned Owls in Argentine Patagonia. However, our results reinforce their explanation for the low frequency of lagomorphs in the diet of Patagonian Great Horned Owls as compared to horned owls at similar latitudes in the northern hemisphere, where they

Table 2. Biomass of rodents in Great Horned Owl diets in Argentina expressed as a percent of the total biomass of rodents consumed in each season. Mean prey weights were obtained from Pearson (1983) for *C. macrouryx*, *G. valdivianus* and *I. tarsalis*; from Pearson (pers. comm.) for *C. haigi*, and from Trejo (unpubl. data) for the remaining species.

PREY	ABL	ABX	ELI	LOX	CHE	REI	OLI	GEO	IRE	CTE
1995										
Summer	5.2	2.8	17.1	3.0	—	42.2	18.1	—	—	11.6
Autumn	7.5	0.4	8.4	15.0	—	40.9	12.2	—	—	15.6
Winter	12.8	5.6	13.2	7.7	—	43.5	7.2	—	—	10.0
Spring	32.6	2.2	11.5	6.7	0.8	6.9	13.1	—	—	26.2
1996										
Summer	25.4	7.0	18.0	3.1	—	22.3	8.0	—	—	16.2
Autumn	14.9	2.0	22.7	—	—	16.9	10.1	1.2	—	32.2
Winter	13.5	7.3	11.6	—	—	27.9	7.8	—	—	31.9
Spring	24.3	3.0	10.7	6.3	—	37.4	5.0	—	1.2	12.2
TOTAL %	18.9	3.9	13.7	6.0	0.2	29.0	10.2	0.1	0.1	18.0
Prey mean	28.1	15.3	16.6	56.2	66.8	63.8	25.4	27.8	41.3	146.2

ABL, *Abrothrix longipilis*; ABX, *Abrothrix xanthorhinus*; ELI, *Eligmodontia morgani*; LOX, *Loxodontomys micropus*; CHE, *Chelemys macrouryx*; REI, *Reithrodont auritus*; OLI, *Oligoryzomys longicaudatus*; GEO, *Geoxus valdivianus*; IRE, *Irenomys tarsalis*; CTE, *Ctenomys haigi*.

weigh on average 30–40% more. Donázar et al. (1997) suggested that the large size of adult lagomorphs could constrain Patagonian horned owls from preying on them, while large rodents and young lagomorphs may be more easily handled.

E. morgani, the mouse consumed most frequently numerically and whose biomass had least seasonal variation, would not seem to be a profitable prey due to its low weight (20 g). The energetic cost of capturing and handling these mice may exceed the actual gains (Jaksic and Marti 1984). Nevertheless, *E. morgani* was abundant in the area (Guthmann 1996) and vulnerable, the two conditions that Jaksic and Marti (1984) consider appropriate for such small prey to be included in the diet of *Bubo* owls. It is easy to catch because it inhabits sites with little plant cover or bare ground and it runs in the open for prolonged periods (Trejo pers. obs.). The prey that supplied the greatest biomass in our study was *Reithrodont* spp. According to Pearson (1988), its nocturnality, long hours of feeding, open habitat, and unwary behavior seem to expose it to predation by owls and other nocturnal predators. *Ctenomys haigi*, the largest rodent in the area, was eaten in low numbers likely due to its fossorial habits. *O. longicaudatus* and *L. micropus*, which inhabit areas covered by bushy vegetation, are scansorial (Pearson 1983, 1995), which could facilitate their detection and capture by owls.

Although only one specimen each of *Irenomys tar-*

alis, *Chelemys macrouryx* and *Geoxus valdivianus* were found in the pellets, their occurrence was noteworthy because none of them were captured during the three years over which Guthmann (1996) systematically trapped rodents at the same site where we collected pellets. All three species are typical of the forest and environments with high plant coverage (Pearson 1983, 1995). Their occurrence in the diet indicated that they may have been present in the area in low numbers, or perhaps the fossorial habits of *G. valdivianus* and *C. macrouryx* made them difficult to capture.

There was seasonal variation in food-niche breadth. Both the overall food-niche and breeding season (spring and summer) food-niche breadths were similar to those calculated by Donázar et al. (1997) in their study in Junín de los Andes. They estimated a standardized food-niche breadth of 0.20 for the breeding season. Jaksic et al. (1986) found that the horned owl diet breadth in Chile declined from north to south based on standardized food-niche breadth measurements obtained for three Chilean locations at different latitudes: La Dehesa, 33°21'S ($FNB_{st} = 0.66$), Puerto Ibáñez, 46°18'S ($FNB_{st} = 0.62$) and Torres del Paine, 51°S ($FNB_{st} = 0.24$). However, the $FNB_{st} = 0.20$ obtained both for Junín de los Andes (39°30'–40°20'S, 70°30'–71°30'W, Donázar et al. 1997) and for Bariloche (41°08'S, present study) does not fit within the latitudinal trends proposed for Chile.

The $FNB_{st} = 0.60$ obtained by Iriarte et al. (1990) for Torres del Paine is also at odds with the proposed latitudinal trend. Considering the seasonal fluctuations in the composition of the diet, comparisons between different locations should probably be done using data from the same time of year.

In our study, the five species most consumed by horned owls had minimum population levels in winter, while in other seasons they reached peak numbers (Guthmann et al. 1997). This would explain the increase of the food-niche breadth in winter caused by the greater evenness, since the availability of all prey species.

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SHORT COMMUNICATIONS

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HABITAT USE OF CROWNED EAGLES (*HARPYHALIAETUS CORONATUS*) IN THE SOUTHERN LIMITS OF THE SPECIES' RANGE

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KEY WORDS: *Crowned Eagle*, *Harpyhaliaetus coronatus*; *habitat use*, *Argentina*.

The breeding range of the Crowned Eagle (*Harpyhaliaetus coronatus*) is limited to semi-open woodlands in lowlands and moderate altitude mountain ranges of Argentina, Bolivia, Brazil, Paraguay, and Uruguay. It is a large-sized, open country raptor that eats a variety of vertebrate prey species. There are over 112 sight records for the species, most of them from Argentina over the past 50 years, including relatively recent encounters in Lihue Calel (province of La Pampa) in the southern limit of the species' range (Collar et al. 1992, De Lucca 1992 and 1993). Based on this, it appears that the Crowned Eagle mainly occurs in the northcentral part of the country, in open woodlands and savannas. Three nests have been described in Argentina. All contained a single egg (Giai 1952, de la Peña 1992). The Crowned Eagle has been protected in Argentina since 1954 and in Brazil it is listed as a Threatened Species (Chebez 1994). Little is known, however, about its ecology and behavior (Collar et al. 1992, Salvador and Eroles 1994, Gil et al. 1995).

Here, we provide new information on the Crowned Eagle's habitat requirements by describing the habitats it uses for roosting and nesting in the southern limits of its range.

MATERIALS AND METHODS

Our study was conducted during 1996–97 in an area covering approximately 5000 km² centered in Lihue Calel National Park (37°54'S, 65°39'W), province of La Pampa, Argentina. The area is situated at the ecotone between savanna dominated by *Prosopis caldenia* and shrubland dominated by *Larrea* spp. Since the 19th century, the natural landscape has been gradually modified by afforestation followed by extensive ranching. Currently, natural woodlands occur primarily in depressions and ravines, and shrublands with isolated *P. caldenia* or small woodlots characterize the landscape. Fire is a common natural disturbance and it is often prescribed to improve grass productivity. The climate is semiarid; mean temperature of the warmest and coolest months is 25°C and 9°C, respectively, and the mean annual precipitation is 414 mm.

Because we expected the Crowned Eagle to be difficult to see, we conducted both road surveys and interviews with local farmers to locate eagle roosting areas. Additionally, staff at the Lihue Calel National Park was instructed to look for and report any encounter with Crowned Eagles. Road surveys were conducted along six 50-km transects, completing one observation stop of 5 min every 0.8 km (Fuller and Mosher 1987). Surveys were performed by the same observers, during 18–24 November 1996 from 600–1300 H. A total of 20 farmers were interviewed. We asked them whether they had seen Crowned Eagles. If the answer was yes, we asked for a description of the animal. If the description fit a Crowned Eagle, we proceeded to fill out a questionnaire asking the following questions: (1) When did you see the eagle?; (2) Where did you see it?; (3) In what type of habitat?; (4) From where did you see the eagle?; (5) Was the eagle dead or alive?; and (6) What was the eagle doing? After completing the questionnaire, we asked farmers to bring us to the exact locations where eagles were observed. The following variables were recorded in 1-ha square plots centered on the points where eagles were seen: habitat type, number of vegetation strata, canopy cover, canopy height, dominant tree species, shrub cover, shrub height, dominant shrub species, understory cover, understory height, and dominant herbaceous plants.

RESULTS AND DISCUSSION

Three new records for the Crowned Eagle were reported by staff of the National Park of Lihue Calel in 1996–97. On 18 November 1996, an eagle was observed perched in a tree approximately 20 km east of the Lihue Calel National Park. A second sighting was made on 22 November 1996 approximately 40 km southeast of the park. The third sighting was of a subadult Crowned Eagle on 21 September 1997 perched in a *Prosopis* tree in the park.

No Crowned Eagles were recorded during road surveys. Of the 20 farmers interviewed, 10 said they had seen Crowned Eagles and their descriptions fit the eagle's features. All of the farmers referred to the large size and head feathers, and most of them recalled the eagle's

characteristic whistle and reluctance to fly off when approached. Eagles were encountered while farmers were walking (40%), driving (30%) or riding horses (30%). Most eagles were observed in natural woodlands (50%) or near *tajamares* (40%, artificial ponds surrounded by trees that provide water for cattle). Eagles were seen perched (80%), flying (10%) or perched and eating. Four encounters were not considered in the analysis, one of them because it had occurred about six years prior to the interview (all other sightings were in 1996–97). The remaining three cases were not used because farmers were unable to determine the exact location where they saw eagles. No farmer recalled the encounter date and no dead eagles were reported.

Vegetation in all roosting habitats consisted of three strata. The dominant tree species was *P. caldenia*. Canopy cover was $37 \pm 18\%$ ($\bar{x} \pm 1$ SD) and canopy height was 6.2 ± 2.6 m. Dominant shrub species were *Larrea nitida* (present in 67% of the described sites), *Lycium chilense* (17%) and *Prosopis flexuosa*. Other shrub species included *Larrea divaricata* (in 67% of the sites), *Condalia microphylla* (67%), *Chuquiraga erinacea* (50%), followed by *Geoffroea decorticans*, *Schinus fasciculatus*, *Prosopidastrum globosum* and *Lycium gilliesianum*. Shrub cover and height were $17 \pm 16\%$ and 1.6 ± 0.2 m, respectively. The understory was dominated by grasses (*Stipa gynerioides* and *S. tenuissima*) in five of the described sites, and by *Verbena aspera* in the remaining site. Sites where Crowned Eagles were seen roosting or nesting appeared to be similar to the typical *tajamar* or woodlots in the area, but different from the matrix of the shrubland landscape.

One nest site was found as a result of our interviews. The nest had been partially destroyed in the summer of 1996 and it did not show any sign of activity on our visit in February 1997. It was located approximately 12 km east of the National Park in a natural 2×4 km forest of *P. caldenia* crossed by a stream. Habitat surrounding the nest tree had 45% canopy cover and a canopy height of 7 m. The middle stratum was dominated by seedlings of *P. caldenia* and by shrub species such as *L. chilense*, *P. flexuosa*, *G. decorticans*, *S. fasciculatus*, and *C. microphylla*. Mean shrub cover was 25% and mean height was 1.5 m. The understory was dominated by *Stipa gynerioides*, *S. tenuissima*, and *Baccharis ulicina*. Percent cover of herbaceous plants was 25% and height was 0.4 m. The nest was a large platform of sticks placed 6 m high in a 12 m *Prosopis* tree. It was supported by two branches and was built with *Prosopis* branches that measured 0.6–2.2 cm in diameter. Previously, Giai (1952) described two Crowned Eagle nests built on communal nests of Monk Parakeets (*Myiopsitta monachus*) and De la Peña (1992) described a large platform nest 5 m up in an *Eucalyptus* tree. Our results show that Crowned Eagles may build nests in shorter and less conspicuous trees than those dominating northern savannas.

Our sightings were consistent in that Crowned Eagles were observed using primarily *P. caldenia* for roosting and

habitats that provide for tree, shrub and grass cover. The southern limit of the species' range appears to be at the ecotone between the phytogeographic provinces of *Espin-al* and *del Monte*, that occur through the NE–SW gradient of decreasing mean annual precipitation in Argentina. The *Espin-al* is a savanna dominated by *Prosopis* sp. and *del Monte* is characterized by shrublands dominated by *Larrea* sp. with isolated *Prosopis* and isolated woodlots occurring mainly in depressions and ravines.

Crowned Eagles seem to depend on the presence of trees because they do not occur south in the Patagonian steppe. In the southern limit of its range, the Crowned Eagle occurs in a fairly transformed landscape characterized by shrublands with isolated groups of native trees providing nesting and roosting habitats. This finding has conservation implications for Crowned Eagles. Current land management in the area includes afforestation followed by ranching. Creation of extensive areas lacking trees or having isolated trees may result in the reduction of the eagle's range. Conservation efforts should include the provision of native woodlots due to their importance for Crowned Eagles.

RESUMEN.—En este estudio aportamos nueva información acerca de los requerimientos de hábitat del águila coronada (*Harpyhaliaetus coronatus*), a través de la descripción de los sitios usados como posadero en el límite sur del área de distribución de la especie. Adicionalmente, aportamos tres nuevos registros y describimos un nido. Los sitios donde las águilas fueron vistas eran similares a un típico *tajamar* (laguna artificial redeada de árboles) o a un monte, pero diferentes a la matriz del paisaje de tipo arbustiva. La vegetación presentaba tres estratos, donde *Prosopis caldenia* (caldén) era la especie arbórea dominante. La cobertura de la canopia era de $37 \pm 18\%$ (promedio ± 1 DE) y la altura de 6.2 ± 2.6 m. Las especies arbustivas dominantes eran *Larrea nitida*, *Lycium chilense* y *Prosopis flexuosa*. La cobertura y altura de arbustos era de $17 \pm 16\%$ and 1.6 ± 0.2 m, respectivamente. El estrato bajo estaba dominado por pastos. La creación de áreas extensas sin árboles o con árboles aislados podría resultar en la reducción del área de distribución de la especie. Esfuerzos de conservación requerirán de un manejo del hábitat que provea grupos de árboles nativos.

[Traducción de Autores]

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A COMPARISON OF METHODS TO EVALUATE THE DIET OF GOLDEN EAGLES IN CORSICA

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KEY WORDS: *Golden Eagle*, *Aquila chrysaetos*; *diet*; *Corsica*.

Identification of prey remains, pellet analysis and direct observation of prey deliveries are the principal methods used to study the diets of nesting raptors (Marti 1987). Although it is often best to observe or film nests for long periods to quantify prey deliveries, this is not always possible due to time and logistical constraints. To assess the validity of using prey remains and pellets as a means of determining diet, several authors have compared data from collections of nest contents with data obtained from direct observation for various raptor species (Collopy 1983, Simmons et al. 1991, Mersmann et al. 1992, Mañosa 1994, Real 1996). Overall, they have found that by combining remains and pellets, collected with the same level of effort, it is possible to determine

diet. Previous studies of the diet of Golden Eagles (*Aquila chrysaetos*) in the Mediterranean area have been based on the collection of prey remains, without taking into account any possible biases in the data collected using only this technique (Handrinos 1987, Cheylan 1983, Fasce and Fasce 1984, Fernandez 1991, Grubac 1987, Huboux 1984). Considering that the variety of food resources on Mediterranean islands is limited (Seguin and Thibault 1996) with a moderate spectrum of potential prey, we conducted this study to determine the best methods for monitoring the diet of Golden Eagles on Corsica.

STUDY AREA AND METHODS

Corsica (42°N, 9°E) is one of the major islands in the western Mediterranean covering an area of 8750 km². It supports a breeding population of 32-37 pairs of Golden Eagles (Torre 1995). Our study area, in the Verghello

Table 1. Minimal Number of Individuals (MNI), percentage of different prey according to different diet analysis methods and correction factors (c.f.) for a Golden Eagle nest in Verghello Valley (Corsica), 1992, 1994, and 1995

	DELIVERED PREY N = 79			REMAINS N = 52			PELLETS N = 50			REMAINS + PELLETS N = 72		
	N	%	N	%	c.f.	MNI	%	c.f.	MNI	%	c.f.	
Mammals												
Large mammals	31	39.2	30	57.7	+1.47	25	50.0	+1.28	32	44.4	+1.13	
Small mammals	6	7.6	1	1.9*	-4.00	3	6.0	-1.27	4	5.6	-1.36	
Birds												
Corvidae	10	12.7	11	21.2	+1.67	2	4.0*	-3.37	11	15.3	+1.20	
<i>Alectoris rufa</i>	3	3.8	6	11.5*	+3.03	2	4.0	+1.05	6	8.3*	+2.18	
Others	2	2.5	1	1.9	-1.32	3	6.0*	+2.4	4	5.6*	+2.24	
Reptiles												
<i>Coluber viridiflavus</i>	27	34.2	3	5.8*	-5.9	15	30.0	-1.14	15	20.8	-1.64	

* Significantly different from the frequencies of delivered prey.

Valley, included one breeding pair that had been monitored by the Parc Naturel Régional de Corse since 1981.

We observed prey brought to this nest by adult eagles from mid-May to late July in 1992, 1994, and 1995. During the three years, hatching occurred between 15–24 May and fledging occurred between 28 July–4 August. We made observations using a 20–60× spotting scope from a blind located 200–250 m from the nest. Observers came to and left from the blind at night in order not to disturb the adults. Observations were made for 1 d every 2.5 d with observation days evenly distributed between hatching and fledging for a total of 1271 observation hr spread over 82 d (1992—27 d, 1994—23 d, and 1995—32 d). Whenever possible, prey items were identified to species and the identification was relatively easy because the number of mammalian species likely to be taken by Golden Eagles was low (15 taxa included eight domestic, Saint-Girons 1989, Raveneau 1993). However, not all prey could be identified due to poor visibility during observation periods caused by heat, haze, and aggressive behavior of the young as they took prey from adults. Domestic goat (*Capra hircus*) and sheep (*Ovis aries*) could not be differentiated in any cases, so they were grouped as Caprini.

In each of the three years, remains were carefully collected in and under the nest in late August after fledging. Pellets were dissected and separated into bone fragments, feathers, reptile scales, and hair. Bones collected in the nest or extracted from pellets were identified by comparison with osteological collections (Muséum National d'Histoire Naturelle, Paris, France) following methods of Payne (1985), Barone (1986), and Vigne (1995). Feathers (both from the nest or extracted from pellets) were identified by comparison with a reference collection. Hair was identified by comparison with Spillmann (1991). Because adults spent most of the time away from the nest after the young were 4-wk old, we assumed that most pellets we collected from the nest were from the young. Each species identified in a pellet was counted as an individual.

Quantification of food remains was based on minimum number of individual estimates (MNI) (Poplin 1976, Vigne 1991) based on the number of the most frequent anatomical part in food remains or the pairing of anatomical parts (e.g., jaws). The drawback of this method is that it is impossible to be totally objective in the pairing of bone pairs. Also, the most frequent species are underestimated in comparison to rare species (Poplin 1976). Prey were separated into six categories: large mammals (Caprini, boar [*Sus scrofa*] and red fox [*Vulpes vulpes*]), small mammals (weasel [*Mustela nivalis*]), European hedgehog [*Erinaceus europaeus*]), and black rat [*Rattus rattus*]), birds (Corvidae, Red-legged Partridge [*Alectoris rufa*] and other birds), and snakes. Differences between taxa, years or prey categories obtained by both methods were tested with Chi-square contingency tables.

RESULTS AND DISCUSSION

Of the prey delivered to the nest, 86% (N = 79, Table 1) were whole. The remainder consisted of portions of large mammals (Caprini, boar and unidentified mammals). Altogether, 39% of the prey delivered to the nest was large mammals, 8% was small mammals, 19% was birds including Red-legged Partridges, Common Kestrels (*Falco tinnunculus*), an unidentified raptor nestling, pigeons (*Columba* spp.), Common Raven (*Corvus corax*), and Eurasian Jay (*Garrulus glandarius*), and 34% was snakes (western whip snake [*Coluber viridiflavus*]). No significant difference appeared among the three years in the amount of these different prey that was delivered to the nest ($\chi^2 = 3.23$, df = 6, $P = 0.78$). Analysis of prey remains collected at the nest showed the diet consisted of 44% large mammals, 6% small mammals, 29% birds, and 21% snakes. Again, no significant difference was found in the diet among the three years ($\chi^2 = 4.44$, df = 6, $P = 0.67$).

Bones contributed most data for the quantitative as-

Table 2. Minimal Number of Individuals and number of species (in parentheses) obtained from bone identification and complementary data by pellet and feather examination from material collected in a Golden Eagle nest in Verghello Valley (Corsica), 1992, 1994, and 1995.

	BONES	PELLETS	FEATHERS
Large mammals	30 (4)	3 (0)	—
Small mammals	1 (1)	3 (1)	—
Large birds	10 (2)	0 (0)	4 (1)
Small birds	0 (0)	1 (1)	9 (3)
Reptiles	3 (1)	12 (0)	—

essment of MNI for large mammals and large birds (Table 2). Pellets provided little additional information for large mammals, but added additional data for estimating MNI for small mammals and snakes. Feathers provided supplementary data on bird numbers, especially on smaller species. Analysis of bones yielded the most information on the number of species while pellet analysis better predicted occurrence of small mammals and birds (Table 2). Feathers provided the best estimate for small bird species.

Comparison of data obtained for prey delivered to the nest with that of prey remains showed a significant difference between the six categories of prey ($\chi^2 = 19.43$, $df = 5$, $P = 0.002$). The number of mammals and reptiles in the diet was underestimated, while birds are overestimated in samples of prey remains. In fact, the frequency of small mammals was four times lower in remains than in prey delivered. Red-legged Partridge, in contrast, were three times more frequent and western whip snakes were six times less frequent. The small mammals, the Red-legged Partridge and the western whip snake contributed to the significant difference between prey delivery and remains. The comparison between prey delivered and pellets was not significant among the six prey categories ($\chi^2 = 4.51$, $df = 5$, $P = 0.48$). Nevertheless, the Corvidae were three times less frequent in pellets than in prey deliveries. On the other hand, the frequency of birds (except the Corvidae and the Red-legged Partridge) in pel-

lets was 2.4 times greater than in prey deliveries. The comparison between prey delivered and remains plus pellets was not significant among the six prey categories ($\chi^2 = 5.03$, $df = 5$, $P = 0.41$). Nevertheless, the Red-legged Partridge and other birds were two times more frequent than in the prey delivered.

Using all methods, 15 species of prey were identified (Table 3). Here also, there was no significant difference in the species composition of the diet estimated by direct observation or by analysis of remains and pellets ($\chi^2 = 6.51$, $df = 2$, $P = 0.99$).

One might expect that food habits data collected once at the end of the nesting season would be biased in favor of large prey species. However, when adult Golden Eagles clean nests, females often eliminate the larger remains which could result in an underestimation of large prey species (Mathieu and Choisy 1982, Tjernberg 1981). This bias has been noted for other species (Real 1996).

Several sources of bias exist in the results of prey analysis based on remains only that are related to prey size and factors affecting fragmentation of remains such as removal when remains are taken out of nests by females, difficulties in identification owing to wear, differences in the size of prey, and destruction of osteological remains. These factors probably explain the differences we observed between the prey delivery and prey remains methods. One of the more important biases we found in the collection of prey remains of Golden Eagles was the underestimation of the small prey items, in particular small mammals and reptiles, because most of the time they were completely eaten. This bias has been previously observed in Golden Eagle dietary studies (Delibes et al. 1975, Mathieu and Choisy 1982, Tjernberg 1981), and of other raptors (Simmons et al. 1991, Mersmann et al. 1992, Mañosa 1994, Real 1996). Birds such as Red-legged Partridges are overestimated because of the abundance of sterna and feathers. Pellets overestimated birds other than corvids and Red-legged Partridges in the diet because they were eaten entirely. Assuming that the occurrence of a prey species in a pellet corresponds to an individual can also overestimate the number of large mammals in the diet since several pellets could contain the remains of the same individual of a prey taxon eaten

Table 3. Overall number and percentage of species identified by the different diet analysis methods (prey delivered, remains, pellets, and remains + pellets), at the Golden Eagle nest in Verghello Valley (Corsica), 1992, 1994, and 1995.

	DELIVERED PREY		REMAINS		PELLETS		REMAINS + PELLETS	
	N	%	N	%	N	%	N	%
Mammals ($N = 6$ species)	5	83.3	6	100.0	4	66.7	6	100.0
Birds ($N = 8$ species)	5	62.5	6	75.0	5	62.5	7	87.5
Reptiles ($N = 1$ species)	1	100.00	1	100.0	1	100.0	1	100.0
Total ($N = 15$ species)	11	73.3	13	86.7	10	66.7	14	93.3

over several days. No method gives a perfect estimate of the nesting diet but combining remains and pellets seems to be the least biased estimator of diet available if deliveries cannot be recorded. The complementary nature between these two types of prey analysis has been shown in previous studies on raptor diet (Simmons et al. 1991, Mersmann et al. 1992, Mañosa 1994, Oro and Tella 1995, Real 1996).

The comparison of direct observations and collection of prey remains to determine the diet of Golden Eagles was studied by Collopy (1983), but in a region where the largest prey was jackrabbits (*Lepus californicus*). Our study was the first to compare the different analytical methods in an area where prey are larger than Leporidae. While either method gave similar results for the percent frequency of prey in the diet of Golden Eagles, periodic observations of food delivered to nests are necessary if the main objective is estimate prey biomass (Collopy 1983), or to obtain information on selection of prey (Real 1996). Our data indicate that the combination of prey remains plus pellets collected on only one visit after the breeding season would enable the study of several pairs of eagles over a large area and a short period of time.

RESUMEN.—Numerosos estudios sobre el régimen alimenticio del pollo de Aguila real (*Aquila chrysaetos*) están basados en el análisis de los restos óseos o de las egagrópilas. Pero, dado que dichos restos sufren una degradación diferencial, los resultados pueden quedar sesgados. Desde esta óptica hemos comparado durante cuatro períodos de reproducción, en una isla mediterránea, los restos de huesos, de egagrópilas y de plumas encontrados en un nido a los datos obtenidos por observación directa. Queda comprobado que los diferentes tipos de restos se complementan, y que por consiguiente su recogida y análisis con el mismo esfuerzo son necesarios para que la descripción del régimen alimenticio del pollo de Aguila real se acerque en lo posible de la realidad.

[Traducción de Pedro Arrizabalaga]

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A RECORD OF A HARPY EAGLE FROM EASTERN PARAGUAY

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KEY WORDS: *Harpy Eagle*; *Harpia harpyja*; *Paraguay*; *sight record*.

On 2 August 1995, I recorded an immature Harpy Eagle (*Harpia harpyja*) in rainforest at Reserva Privada Itabó (24°20'S, 54°35'W), Departamento Canindeyú, Paraguay. The Harpy Eagle is poorly known in Paraguay and has not been previously recorded at this site.

I first sighted the perched eagle in an emergent tree beside the main road through the reserve. It had been forced into the tree by a flock of seven White-eyed Parakeets (*Aratinga leucophthalmus*). After 10 min, the bird was again mobbed by the parakeet flock, causing it to fly off into the adjacent forest canopy.

There was no question that the bird was a Harpy Eagle. Its most obvious feature was its large, completely creamy-white facial disc. Its bill was dark grey and its eyes large and black. Several completely white feathers formed a crest on its head. Its breast and belly were a uniform creamy white except for a pale grey area across its breast. The undertail appeared dark brown and the underwings appeared pale with some dark barring. I hardly saw the upperparts but they appeared to be largely grey, at least

on the back, scapulars and wing coverts, with black lower on the wings. I did not see the upperwings or uppertail in flight.

Not all of the salient characters, notably the enormous tarsi and the divided crest could be seen due to the angle of observation. However, nothing about the bird indicated that it was a Crested Eagle (*Morphnus guianensis*). Immature Crested Eagles are distinguished from immature Harpy Eagles by their slimmer bodies, long tails, smaller bills, dark lores, black-tipped crests and long, relatively small tarsi. Light phase Crested Eagles also have white underwing coverts contrasting with barred remiges (Hilty and Brown 1986). Crested Eagles have not been recorded in Paraguay (Hayes 1995), although they have been historically recorded in Misiones Province, Argentina (Narosky and Yzurieta 1987).

I excluded other large raptors such as Mantled Hawk (*Leucopternis polionota*), Black-and-white Hawk-Eagle (*Spizastur melanoleucus*), Black Hawk-Eagle (*Spizaetus tyrannus*) and Ornate Hawk-Eagle (*S. ornatus*) based on the size and bulk of the bird alone and the plumage of the bird I observed did not match the plumages of any of these species (Narosky and Yzurieta 1987). The latter three species are known from Reserva Privada Itabó (Lowen et al. 1996).

The Harpy Eagle is rare throughout its range from Mexico to Argentina. It was considered Globally Threat-

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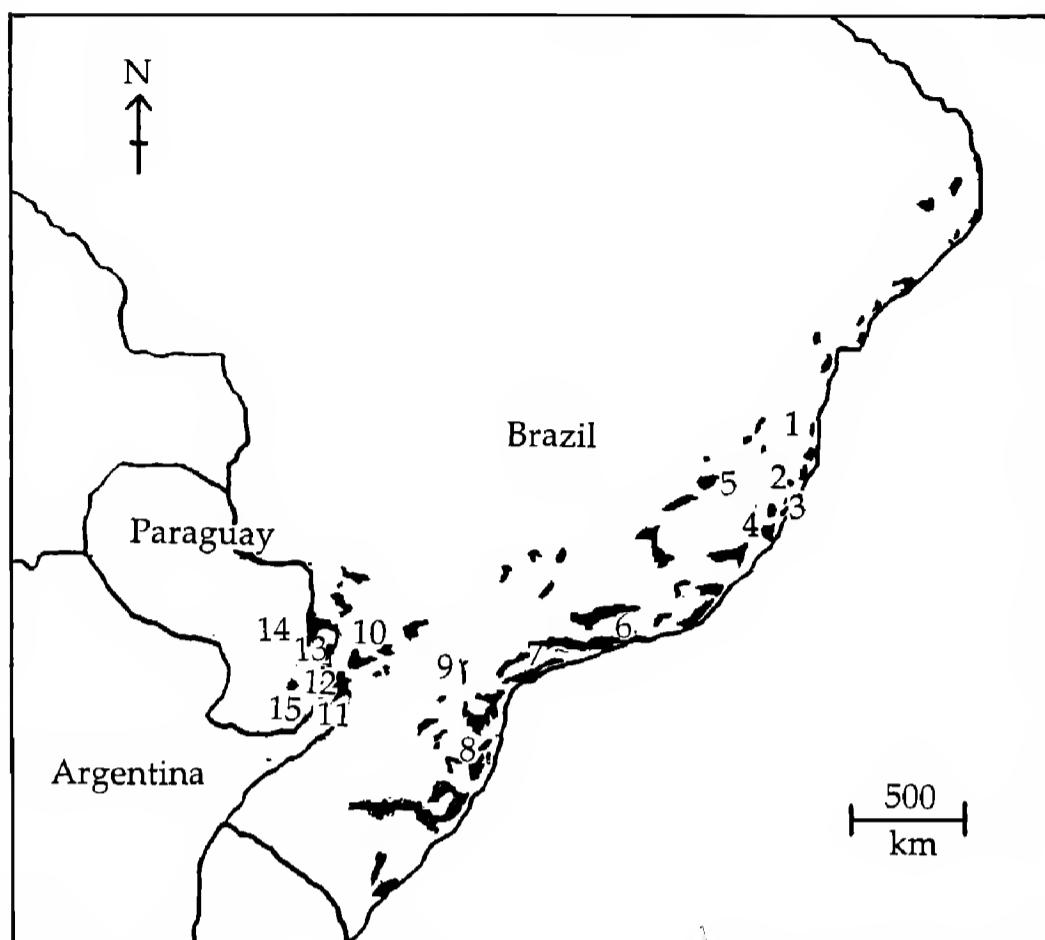


Figure 1. Forest cover and some recent records of Harpy Eagles in the Atlantic forests. Forest cover is shaded dark following Brown and Brown (1992). Recent records of Harpy Eagles are as follows: Brazil (1) Estação Experimental Pau-Brasil, Porto Seguro, Bahia, 1991 (Forrester 1993, Galetti et al. 1997), (2) probable at Sooretama Federal Biological Reserve, Espírito Santo, 1993 (Forrester 1993), (3) Compania Vale do Rio Doce Reserve, Linhares, Espírito Santo, 1992 and 1995 (Forrester 1993, Galetti et al. 1997), (4) probable at Nova Lombardia Federal Biological Reserve, Espírito Santo, 1993 (Forrester 1993), (5) reported without details from Rio Doce State Park and Fazenda Montes Claros, Minas Gerais (Forrester 1993), (6) reported without details from Serra do Mar, Itatiaia National Park and Serra dos Órgãos, Rio de Janeiro (Forrester 1993), (7) Cananéia, São Paulo, 1989, 1990, 1991 and 1993 (Galetti et al. 1997), (8) Parque Estadual da Serra do Tabuleiro, Santa Catarina, 1989 (Albuquerque 1995), (9) Turvo, Paraná, 1984-85 (Bornschein and Straube 1991), (10) Cascavel, Paraná, 1982-83 (Bornschein and Straube 1991); Argentina (11) Misiones, 1980-90s (Chebez et al. 1990, Chebez 1992, De Lucca et al. 1993, De Lucca 1996); Paraguay (12) Itaipú Biological Reserves, Alto Paraná, 1990s (Gill Morlis et al. 1995), (13) Reserva Privada Itabó, Canindeyú, 1995 (this record), (14) Reserva Natural del Bosque Mbaracayú, Canindeyú, 1994 (Madroño-Nieto and Esquivel 1995), and (15) Caaguazú, 1993 (Lowen et al. 1996).

ened (Collar and Andrew 1988) but it has now been downgraded to Near Threatened (Collar et al. 1992) due to the large amounts of habitat for the species in the Amazonian portion of its range. In southeastern Brazil, it is very rare (Scott and Brooke 1985) and recent records from this region (Fig. 1) range from Bahia (Galetti et al. 1997) south to Santa Catarina (Albuquerque 1995, do Rosário 1996), with scattered sightings in between (Bornschein and Straube 1991, Forrester 1993, Tobias et al. 1993, Sick 1993, Scherer-Neto and Straube 1995, do Rosário 1996, Galetti et al. 1997).

The extensive deforestation of Paraná State (Albuquerque 1995) has probably now permanently separated these coastal populations of Harpy Eagles from the inland Paranáense forest of Iguazú National Park, Paraná State (Brazil), Misiones Province (Argentina) and eastern Paraguay. Forrester (1993) did not list any records for

Iguacu National Park, Paraná State, Brazil and Saibene et al. (1996) did not list the species for Iguazú National Park, Misiones Province (Argentina). However, Harpy Eagles have recently been found nesting at higher altitude sites elsewhere in the province, in Departamentos San Pedro, Eldorado and Iguazú (Chebez et al. 1990, Chebez 1992, De Lucca et al. 1993, De Lucca 1996).

Hayes (1995) lists seven records of Harpy Eagles from a wide range of locations in Paraguay, although none of these are supported by published descriptions or specimens. In addition, there is a recent sight record from the Itaipú Biological Reserves in Departamento Alto Paraná (Gill Morlis et al. 1995, Scherer-Neto and Straube 1995). Madroño-Nieto and Esquivel (1995) recorded an immature Harpy Eagle at Lagunita in the Reserva Natural del Bosque Mbaracayú, Departamento Canindeyú in 1994 and an eagle was reported in Caaguazú in 1993 (Lowen

et al. 1996). The species is considered Endangered in Paraguay (CDC 1990).

The Reserva Privada Itabó covers 3000 ha of forest which is sustainably harvested for palmito hearts of palm (Brooks et al. 1993). The concentration of fruiting palms at the site attracts large numbers of frugivorous birds and mammals, which in turn support high densities of carnivores (Lowen et al. 1995). Presence of an immature Harpy Eagle potentially indicates that the species breeds at Itabó. However, the lack of other records at the site (Lowen et al. 1996) suggests that this bird was more probably a wandering individual attracted to the site by the abundance of food. Albuquerque (1995) similarly felt that individual Harpy Eagles move between *Araucaria* groves with the seasonal abundance of prey, and until 1958 "migrant individuals" occurred in summer in Rio Grande do Sul State, Brazil (Sick 1993). Whatever the explanation for the presence of the individual at Itabó, this record supports the conclusion that Reserva Privada Itabó is of key importance for bird conservation in Paraguay (Lowen et al. 1995).

RESUMEN.—El 2 de agosto de 1995 registré un ejemplar juvenil del águila harpía (*Harpyia harpyja*) en la selva de la Reserva Privada Itabó (24°20'S, 54°35'W), Departamento Canindeyú, Paraguay.

[Traducción de Autor]

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LETTERS

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DUST BATHING IN THE BEARDED VULTURE (*GYPAETUS BARBATUS*)

The source of the rufous coloration of adult Bearded Vultures (*Gypaetus barbatus*) has been a point of debate. In some cases, variations in this coloration have been used as a systematic character to establish new subspecies (Fatio 1899, *Faune des Vertebres de la Suisse.*, Vol. 2; Fischer 1963, *Die eier. Neue Brehm-Bucherei, Wittenberg*). Several studies have in fact confirmed that the rusty coloration of underparts and the neck and head of adult birds is due to iron oxides derived from weathered dolomitic limestone (Volker 1960, *Fortschr. Chem. org. Natstoffe* 18:107–110; Berthold 1967, *Zool. Jb. Syst.*; Brown and Bruton 1991, *J. Zool. Lond.* 223:627–640; Houston et al. 1993, *Äull. B.O.C.* 113(4):260–263). Apparently, Bearded Vultures acquire the red-orange coloration passively as they roost at night on their bellies on rock ledges rich in iron compound (Berthold 1967, *Zool. Jb. Syst.*; Siegfried and Frost 1973, *Bonn. Zool. Beitr.* 24:387–393). Such staining of breast and neck feathers has been argued by Clancey 1968 (*Bokmakierie* 20:36–37) since no bird has ever been recorded dusting in the wild. In fact, radio-tagged vultures in South Africa and released birds in the Alps have not shown such feather staining (Brown 1988, Ph.D. thesis, Univ. of Natal; Houston et al. 1993, *Äull. B.O.C.* 113(4):260–263).

In captivity, Bearded Vultures develop pure white feathers and are attracted to red soils often dusting or mud bathing (Berthold 1967, *Zool. Jb. Syst.* 93:507–595; Brown and Bruton 1991, *J. Zool. Lond.* 223:627–640). Bathing in water has been reported to be a rather common phenomenon in South Africa but no iron oxides have been found in the pools used by vultures for bathing (Steyn 1982, *Birds of prey of Southern Africa*. Cape Town: David Philip). Although an adult Bearded Vulture was recently reported bathing in the Pyrenees beneath a spring rich in iron oxides (Caussimont et al. 1995, *Bearded vulture annual report*:53), no field observations of birds using dust or mud wallows containing iron deposits have been reported. This may be due to the fact that Bearded Vultures are secretive when visiting such places (Houston et al. 1993, *Äull. B.O.C.* 113(4):260–263).

On 23 March 1997, I observed an adult Bearded Vulture at the Northern slopes of Dikti massif (Eastern Crete, Greece) dust bathing. I had observed it using this location for roosting and sleeping for several months during the winter. The elevation of the roost site was 300 m and the roost itself was located on a 1.5 m shelf on an east-facing cliff of eroded limestone rocks (terra rosa). While observing the bird with a 30× spotting scope from a distance of 300 m, I saw it rubbing its head, neck and chest on the bottom of the ledge. After that, it started pecking and biting and rubbing its head and neck on the rock. This behavior lasted about 8–12 min and finally the vulture laid its belly on the ledge where it spent the rest of the night.

It is quite possible that in arid areas, such as the mountains of Crete where upland streams are scarce and muddy places are completely lacking, Bearded Vultures have no easy access to damp red soils. To acquire their orange coloration, they may rub and peck on rocks to produce dust for dust bathing. They do not appear to eat these dust particles (Brown and Plug 1991, *S. Afr. Zool.* 25(3):169–177) and they do not suffer from calcium deficiency like other scavenging birds (e.g., *Gyps*, Houston 1978, *J. Zool. Lond.* 186:175–184).

If this kind of behavior is indeed the source of pigmentation for feathers of the Bearded Vulture, it is surprising that it has not been recorded more often. The fact that the reddish tones of feathers of Bearded Vultures vary from location to location indicates that feather coloration is passively acquired (Berthold 1967, *Bull. Br. Ornithol. Club* 87: 89–90). On Crete, the intensity of rufous coloration among pairs of Bearded Vultures ranges from dark orange to pure white. In areas with limestone rocks that are resistant to erosion or low annual precipitation (60–80 cm/yr), dirty white or completely white vultures predominate perhaps because dust from dust bathing does not stain the feathers as effectively as does mud and water rich in iron oxides.—**Stavros Xirouchakis, Natural History Museum of Crete, University of Crete, Knossou Ave., Heraklion 71409, Crete, Greece.**

COMMENTARY

EDITED BY DANIEL E. VARLAND

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ON THE EVIDENCE NEEDED FOR LISTING NORTHERN GOSHAWS (*ACCIPITER GENTILIS*) UNDER THE ENDANGERED SPECIES ACT: A REPLY TO KENNEDY

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Kennedy (1997) assessed whether the available scientific evidence supports the claims of declining Northern Goshawk (*Accipiter gentilis*) abundance, which were made in recent petitions (Anonymous 1997) to list the Northern Goshawk as a Threatened Species under the Endangered Species Act (ESA). She analyzed scientific data from published research reports for evidence of a decline in goshawk abundance across North America, including declines in geographic range, population density, nest occupancy, fecundity and survival, and rates of population change. Based on analyses of these variables, she concluded that the available evidence did not support the listing petitioners' claims of declining goshawk abundance across North America.

Congress intended for ESA listings to be based on the best scientific and commercial data available, although the types of data and those qualifying as the best were left up to environmental scientists (Bogert 1994). Lacking internal statutory guidance as to what are the best scientific and commercial data applicable to listing decisions, Carroll et al. (1996) proposed the following standards for prioritizing listing of candidate species: (1) the number of additional species that can benefit from the listing; (2) the species' ecological role; (3) the species' recovery potential; and (4) the species' taxonomic or evolutionary distinctiveness. However, these standards appear to be intended for increasing collateral benefits to the ecosystem and for balancing costs, although the latter would be contrary to the intent of the ESA. None of these standards bear directly on reducing the species' jeopardy of extinction and increasing its chances for survival and recovery in the wild (i.e., conserving the species). Kennedy chose declining abundance of the taxon as her standard, which was a decision warranted by the intent of the ESA. The purpose of my reply to Kennedy is to question both the appropriateness of her choice of variables and her analyses of them when testing for evidence of declining Northern Goshawk abundance.

GEOGRAPHIC RANGE CONTRACTION

A contracting geographic range would indeed signal a likely decline in goshawk abundance. However, the se-

quence of range maps used for concluding such a trend need to be examined carefully for possible biases due to several influential factors. First, as Kennedy speculated, an apparent range expansion in the eastern U.S. could be due to greater efforts at locating goshawks during modern times. A temporal trend in the size of the geographic range cannot be justified as an indicator of goshawk abundance without considering trends in the level of search effort within this range. Second, natural, multiannual shifts in geographic range due to climate or other factors (MacArthur 1972) can appear as unidirectional contractions or expansions when examined over too few years. Third, habitat typically grows more patchy and sparse near a species' range boundary, as does species' abundance (MacArthur 1972, Taylor 1993, Krebs 1994). Accordingly, a number of methods have been used for deciding where to delineate range boundaries (Krebs 1994). Should the range boundary circumvent all breeding populations? All individuals? All habitat patches? Or, should it include only high-quality habitat patches? Perceived temporal trends in range boundary could be due to inconsistent application of multiple range delineation methods. Kennedy (1997) provided no rigorous accounting of these aforementioned methodological problems in comparing geographic range maps through time.

Probably the most useful indicator variable for detecting range contraction is the fraction of area used by the species, which can be measured as the cumulative area either of all occupied habitat patches or of all occupied grid cells overlaid on a distribution map (Gaston 1991, Hanski et al. 1993). However, because species abundance patterns tend to consist of population clusters that shift locations every generation or so (Taylor and Taylor 1977, 1979, den Boer 1981, Hanski 1994), as well as large areas with little or no ecological value to the species (Gaston 1991, Hanski et al. 1993), the fraction of area providing environmental conditions known to serve as high-quality habitat also would be useful for assessing range contraction of Northern Goshawk (Ward et al. 1992, Iverson et al. 1996). Maguire (1993) found that habitat loss contrib-

Table 1. Published estimates of nesting density for Northern Goshawks in North America.

AUTHORS	LOCATION	YEAR	STUDY AREA (km ²)	NO. OF NESTS	NESTING DENSITY (Pairs/km ²)
McGowan (1975)	near Fairbanks, AK	1971	372.0	7.0	0.0188
McGowan (1975)	near Fairbanks, AK	1971	372.0	9.0	0.0242
McGowan (1975)	near Fairbanks, AK	1973	372.0	8.0	0.0215
McGowan (1975)	near Fairbanks, AK	1974	372.0	1.0	0.0027
Shuster (1976)	northern CO, Rocky Mts.	1974	81.0	6.0	0.0741
Shuster (1976)	northern CO, Rocky Mts.	1975	81.0	6.0	0.0741
Bartelt (1977) ^a	Black Hills, SD	1975	448.5	8.0	0.0178
Reynolds and Wight (1978)	western OR	1970	92.8	0.0	0.0000
Reynolds and Wight (1978)	western OR	1971	92.8	0.0	0.0000
Reynolds and Wight (1978)	western OR	1974	117.4	4.0	0.0341
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	8.5	0.9	0.1059
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	12.0	1.2	0.1000
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	22.0	3.0	0.1364
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	27.5	4.0	0.1455
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	29.0	2.1	0.0724
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	36.0	2.4	0.0667
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	44.5	3.3	0.0742
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	50.5	5.1	0.1010
Crocker-Bedford and Chaney (1988)	Kaibab Plateau, AZ	1985	230.0	24.0	0.1043
Kennedy (1989)	Jemez Mts., NM	1986	121.0	7.7	0.0636
Kennedy (1989)	Jemez Mts., NM	1986	273.5	7.7	0.0282
Austin (1993)	Cascades of CA	1989	473.7	9.0	0.0190
DeStefano et al. (1994)	Paisley, east OR	1992	87.8	4.0	0.0456
DeStefano et al. (1994)	Paisley, east OR	1993	129.6	8.0	0.0617
DeStefano et al. (1994)	east Bear Valley, east OR	1992	90.5	8.0	0.0884
DeStefano et al. (1994)	east Bear Valley, east OR	1993	90.5	6.0	0.0663
DeStefano et al. (1994)	west Bear Valley, east OR	1993	105.2	9.0	0.0856
DeStefano et al. (1994)	Spring Creek, east OR	1992	114.0	8.0	0.0702
DeStefano et al. (1994)	Spring Creek, east OR	1993	114.0	3.0	0.0263
DeStefano et al. (1994)	Bly, east OR	1993	106.3	4.0	0.0376
Doyle and Smith (1994) ^b	southwest Yukon	1990	100.0	10.0	0.1000
Woodbridge and Detrich (1994)	Sierran Montane, CA	1989	102.3	11.0	0.1075
Woodbridge and Detrich (1994)	Upper Montane, CA	1989	104.4	6.0	0.0575

^a Reported density estimates from two immediately adjacent areas, which I combined into one area and one estimate.

^b Assumed that the 5 pr they observed comprised only half the population.

uted substantially to a decline in goshawk population viability on the Kaibab Plateau, Arizona. Maguire's population viability analysis (PVA) simulated a declining trend in habitat carrying capacity of 1%/yr and produced certain extinction in goshawk populations, even those with stable or increasing growth rates. Concluding whether the fraction of area used or potentially used by goshawks has changed through time must include knowledge of goshawk habitat and habitat fragmentation, which I will discuss further.

NESTING DENSITY

To evaluate the appropriateness of nesting density for detecting a range-wide abundance trend, I compared 33

nesting density estimates made from 24 study sites spanning the years 1970–93 (Table 1). Estimates of nesting density averaged 0.062 pair per km² (range = 0–0.145, SD = 0.039). The nesting populations studied averaged only 6 pairs of nesting goshawks (range = 0–24, SD = 4.4) on study areas that averaged 148 km² in size (range = 8.5–474, SD = 134).

As noted by Kennedy, estimates of goshawk density have been highly variable. However, her comparison of these density estimates was unlikely to reveal any temporal trends because half the variation in goshawk nesting densities can be explained by the size of the study areas used to make the density estimates (Fig. 1). Similar

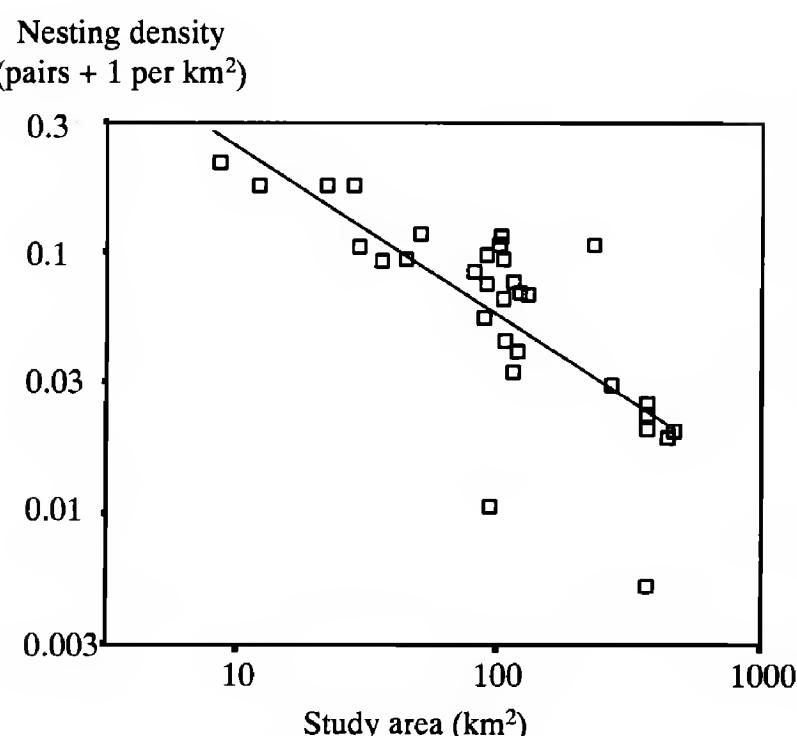


Figure 1. Relationship between nesting density (log of nesting pairs per km^2) and study area size (log km^2 of study area) for Northern Goshawks across North America (see Table 1).

to other species, such as Swainson's Hawks (*Buteo swainsoni*; Smallwood 1995), European Kestrels (*Falco tinnunculus*; Village 1984, Kostrzewska 1988), mammalian primary consumers (Blackburn and Gaston 1996) and mammalian carnivores (Smallwood and Schonewald 1996), published estimates of goshawk nesting density were inversely proportional to the study area ($r^2 = 0.53$, Root MSE = 0.27, $P < 0.0001$):

$$\log \text{Density} = 0.072 - 0.658 \log \text{km}^2 \text{ study area},$$

where density was calculated as the number of nesting pairs plus one, so as to avoid log-transforming 0-values.

The y -intercept of the regression slope predicted 0.18 pair of Northern Goshawks on the average 1 km^2 of habitat area included within the collective study boundaries. This predicted density is about three times as large as the average of reported densities, which is already higher than will be found on the majority of North American forest land units the size of 1 km^2 . My model prediction was absurd. After all, nesting home ranges of 73 adult goshawks averaged 59 km^2 in size and ranged up to 879 km^2 (Bartelt 1977, Kennedy 1989, Austin 1993, Doyle and Smith 1994, Hargis et al. 1994, Keane and Morrison 1994, Iverson et al. 1996). Foraging areas of 50 goshawks averaged 894 km^2 in size and were as large as 2321 km^2 (Hargis et al. 1994, Keane and Morrison 1994, Iverson et al. 1996). The most likely explanation for the excessive density predicted both by the regression model at 1 km^2 (see Smallwood and Schonewald 1996) and by the average among reported estimates was that most investigators selected study sites known in advance to support breeding populations of Northern Goshawk. In fact, the loca-

tions of four of the 10 studies summarized in Table 1 were reportedly selected based on historical records of goshawk nesting or on the distribution of high-quality habitat. At least most of the remaining sites were likely also chosen in one of these ways, rather than randomly. Therefore, estimates of nesting density were made for only one aspect of the population: the high-density cluster. Without long-term sampling across large geographic areas, including the majority of the forest landscapes where goshawks are much rarer, comparisons of nesting density are unlikely to reveal any temporal trend in goshawk abundance across North America.

Further adding to the unsuitability of available density estimates for detecting temporal trends in range-wide goshawk abundance, high-density clusters typically shift locations every generation or so (Taylor and Taylor 1977, 1979, den Boer 1981). A study originally designed around a high density cluster might detect a sudden drop in abundance after a few years. Such a reduction in local density would likely be misinterpreted as a population decline rather than a spatial shift, unless the sampling was of sufficient duration and spatial extent to detect the shift. All but two density estimates included <11 nesting pairs, which in my opinion is barely enough to qualify as a population cluster. The studies generating these estimates have lasted ≤ 9 yr, which is less than a goshawk lifespan and therefore is insufficient for judging persistence (Connell and Sousa 1983). The studies designed to estimate density were not intended to detect population trends across large areas, let alone North America.

REPRODUCTIVE PATTERNS

Fecundity and survival, estimated from local, autonomous studies, also have no necessary relationship with goshawk abundance at the scale of North America. Such estimates represent populations, and have no documented relationship with geographic range size (Gaston 1990) or range-wide abundance. Habitat fragmentation has been proposed as the most likely cause for declines in Northern Goshawk abundance across North America (Crocker-Bedford 1990, Keane and Morrison 1994). However, habitat fragmentation might reduce nest-site occupancy and availability (Crocker-Bedford 1990, Ward et al. 1992, Woodbridge and Detrich 1994), and not fecundity (Woodbridge and Detrich 1994) and survival. Extrapolating Crocker-Bedford's (1990) observed rates of timber harvest and impacts on goshawk nesting on the Kaibab Plateau, habitat loss could conceivably reduce goshawk abundance across North America by 75% during the 75-yr lifetime of a scientific investigator. However, the remaining 25% might reproduce and survive at levels comparable to pre-harvest conditions (Woodbridge and Detrich 1994). The relationships between habitat fragmentation and reproductive success remain unknown except for what has been learned from the stand-thinning studies of Crocker-Bedford (1990) and Ward et al (1992). Like geographic range contraction, widespread

reductions in fecundity or survival across North America would be of concern, but local, autonomous estimates are inappropriate for extrapolation to range-wide estimates of productivity.

TEMPORAL ABUNDANCE TREND

Kirk and Hyslop (1998) recently assessed the status of Canadian raptors by analyzing data from migratory hawk counts, Christmas Bird Counts (CBC), and the Breeding Bird Surveys (BBS) across North America. They found significant declines in the annual number of migrating Northern Goshawks at the majority of migratory hawk count sites in the U.S., although the CBC and BBS showed no such declines. Kirk and Hyslop (1998) acknowledged the hazards of relying on counts of migrating raptors, such as possibly misinterpreting change over several counting years as a trend rather than just as part of a multiannual population cycle. However, changing counts of migrating Northern Goshawks are more likely to be indicative of continent-scale change in abundance through time than would be the rate of population change assessed by Kennedy, because populations are local and may shift locations through time as described previously (Taylor and Taylor 1977, 1979, den Boer 1981).

Kennedy dismissed counts of migrating goshawks because no direct relationship has been established between counts of migrants and the abundance of goshawks across North America. This rationale was not applied to geographic range, population density estimates, nor fecundity and survival, although there was every reason to do so. Her (1997) use of these variables for assessing evidence of a goshawk decline in North America lacks scientific foundation, but serves as a first step in the needed scientific debate on the evidence needed to conclude whether a species is declining across its geographic range.

HABITAT FRAGMENTATION

The relationships between goshawk nesting patterns and forest landscape conditions were not assessed by Kennedy. These relationships also bear on critical habitat designation, which is one of the major steps called for in the ESA listing process, and was originally intended to precede listing decisions (National Research Council 1995). Critical habitat was not defined explicitly in the ESA, but Hall et al. (1997) defined this habitat as the geographic areas providing the resources necessary for breeding and population persistence, consistent with the concept of high-quality habitat. Although critical habitat has yet to be designated for the Northern Goshawk, the available research reports indicate that "mature," "closed-canopy," or "old-growth" forest will likely comprise a good part of the critical habitat designation (Crocker-Bedford and Chaney 1988, Ward et al. 1992, Graham et al. 1994, Iverson et al. 1996, Beier and Drennan 1997).

Fragmentation of mature forest may be the greatest threat to Northern Goshawks (Keane and Morrison 1994, Woodbridge and Detrich 1994, Iverson et al. 1996). Habitat fragmentation is the reduction in and increased isolation of available habitat (Wilcox and Murphy 1985). In general, habitat fragmentation has been widely acknowledged as the greatest threat to the survival of many species (Wilcox and Murphy 1985). Habitat fragmentation should be given the greatest scrutiny in making listing decisions, and its possible impact on the goshawk is measurable indirectly using historical and recent maps of mature forests (Ward et al. 1992).

However, habitat fragmentation must be defined clearly so that it can be made operational with respect to impacts on Northern Goshawks. Hansen and Urban (1992) rated goshawks as highly sensitive to old-growth forest fragmentation based on reproductive effort, nest type, and territory size, but they lacked information on goshawk responses to edge and patch size. Nest-site occupancy was later found positively related to mature forest patch size (Woodbridge and Detrich 1994) and percent canopy closure (Ward et al. 1992), and nesting areas contained less edge between forest and nonforest vegetation types (Iverson et al. 1996). Goshawk habitat must be described carefully using multiscale studies such as conducted and advocated by Keane and Morrison (1994) and Beier and Drennan (1997). Specific resource and habitat patch sizes and their configurations on the landscape must be related to abundance patterns of the species (Kotlier and Wiens 1990, Hanski 1994). The condition of goshawk habitat can then serve to indicate the abundance of goshawks in North America, although predictions of abundance based on the indicator(s) need verification with an extensive sampling and monitoring program (Green 1979).

A metaanalysis, as recommended by Kennedy, probably would not suffice for assessing goshawk abundance trends in North America in lieu of proper sampling (also see Keane and Morrison 1994). I conducted a similar type of analysis for puma (*Puma concolor californica*) density, and found that the autonomy of each population study rendered the collection of studies incapable of providing much insight (Smallwood 1997). Smallwood and Schonewald (1998) since compared all published carnivore population estimates and associated study attributes, but we found the same result: surprisingly little insight into the factors that influence carnivore density, except for the influence of study area on density. Most population studies are not sampling programs *per se*, but rather measurements of population attributes at particular sites and during brief periods of time (relative to the ecological time scale of the species). Comparison of these attributes for temporal trends is inappropriate without controlling for a variety of environmental and study conditions. Such comparison is one form of pseudoreplication (Hurlbert 1984).

An appropriate sampling program would start with a

protocol for selecting multiple sampling sites from various environmental conditions, from which variation in population attributes could be effectively interpreted (Green 1979). The entire geographic range of the taxon is the appropriate spatial scale for sampling that is intended to test for abundance trends and to make taxonomically-based listing decisions. The appropriate sampling protocol for drawing inferences on trends in abundance would involve random or systematic selection of sites throughout the range. Intensive studies of resource requirements at a subset of the sampling sites would need to be linked to the more extensive sampling program so that evolutionary and ecological questions of 'why' and 'how' can be answered, and meaningful conservation strategies put to practice (Keane and Morrison 1994). Such a sampling program may seem daunting, but the case needs to be made that the Northern Goshawk and other species in the U.S. deserve allocation of the necessary funding for sampling at a scale and level of rigor sufficient to achieve the objectives of the ESA.

CONCLUSIONS

Kennedy's decision to pursue evidence of declining Northern Goshawk abundance was more appropriate to the intent of the ESA than were those of Carroll et al. (1996). However, a listing decision for the Northern Goshawk should not rely on the data and analysis she used. Population density, fecundity, survival, and rate of population change all lack scientifically defensible relationships with range-wide abundance, as does the size of the geographic range within a single species (Gaston 1990). The population parameters can be related to local population trends, but their relationships to the trend in range-wide abundance can only be inferred by multiscale study at sites chosen randomly or systematically from across the geographic range. In lieu of appropriate sampling, and in lieu of agreement among scientists for additional variables that should be analyzed, evidence for a Northern Goshawk decline across its range should be based on changes in the availability and contiguity of habitat and migratory counts.

According to Kennedy, the petitioners for the goshawk listing were motivated by their concern for over-harvest of old-growth forest. Regardless of the motivation behind the listing petitions, the listing decision should be based on analysis of the variables that most likely represent a threat to the survival of Northern Goshawks in the wild: the extent of its critical habitat and level of recent habitat fragmentation. Kennedy did not rigorously assess habitat fragmentation as a possible indicator of declining goshawk abundance.

Assessing inappropriate variables for making a listing decision threatens the credibility of the ESA more so than does an ulterior motivation for a listing petition, because the former is an action that can reduce the likelihood of survival and recovery of the species in the wild, whereas the latter is a request that poses no threat to the

goshawk population. That is, applying less than the best scientific data to a listing decision risks committing a Type II error which can have severe conservation ramifications and would be the less ethical choice (Shrader-Frechette and McCoy 1992). Committing a Type I error and inappropriately listing a species as threatened will not reduce the likelihood of its survival, although a delisting in the future can also be time-consuming and damaging to the integrity of the ESA (if listing was unwarranted in the first place). Of course, using the best available scientific data (appropriate variables) would also reduce the chance of committing a Type I error.

Environmental scientists need to develop standards for qualifying scientific data as the best available when making listing decisions, as called for in the ESA. Perhaps Kennedy's paper and my reply can help initiate the needed scientific debate on the methods and variables that are most appropriate for assessing whether a species has declined significantly enough across its range to warrant listing under the ESA.

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THE VALUE OF DEMOGRAPHIC AND HABITAT STUDIES IN DETERMINING THE STATUS OF NORTHERN GOSHAWKS (*ACCIPITER GENTILIS ATRICAPILLUS*) WITH SPECIAL REFERENCE TO CROCKER-BEDFORD (1990) AND KENNEDY (1997)

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Northern Goshawks (*Accipiter gentilis atricapillus*) have long been associated with mature forests, an attribute that has brought them into recent debates over forest management practices. Bent (1937) associated goshawks with extensive forests and large stands of big trees, and more recent research on their nesting habitat found an association with relatively large trees and relatively dense canopies (Shuster 1980, Reynolds et al. 1982, Moore and Henny 1983, Speiser and Bosakowski 1987, Crocker-Bedford and Chaney 1988, Hayward and Escano 1989). Reynolds (1989) described the foraging habitat during the breeding season as older, tall forest where goshawks can maneuver in and below the canopy while foraging. Most of the investigators cited above deduced that timber harvesting could impact goshawks, while others concluded that timber harvest actually had reduced goshawk abundance in portions of some states (Reynolds and Meslow 1984, Mannan and Meslow 1984, Bloom et al. 1985, Kennedy 1988).

I (Crocker-Bedford 1990) reported that the rate of nest reoccupancy in logged areas was 20–25% the reoccupancy rate in areas not logged, despite nest buffers having been left intact in the logged areas. This finding, along with deductions on the effects of timber harvest on the size of the local population, catalyzed additional research

(Squires and Reynolds 1997) and debate. Many scientists (seemingly including Kennedy 1997) and forest managers were left confused over the methods and results of my research. Herein, I assess the strengths and weaknesses of my 1990 paper in order to move the debate on methodologies toward implementation of more productive resource management practices.

Kennedy (1997) emphasized the use of demographic studies in determining whether goshawks warrant Threatened or Endangered status under the United States Endangered Species Act (ESA; United States Government 1988); however, I assert that demographic statistics are unlikely to ever provide sufficient information to determine goshawk status under the ESA. In light of limitations in technology, funding and other problems, this paper suggests an alternative approach to status assessment. Finally, hypotheses are presented on landscape-level habitat needs of goshawks, for use in goshawk status assessment, and as suggestions for further study.

REVIEW OF CROCKER-BEDFORD (1990)

My study area was the North Kaibab Ranger District of northern Arizona. I started nest monitoring in 1982 under a study plan having the objective of comparing the efficacy of different-sized no-cut nest buffers for goshawk

habitat protection. During 1973–84, U.S. Forest Service personnel located at least one goshawk nest within each territory discussed in my 1990 paper. I reported on reoccupancy during 1985–87 of individual nest trees and territories. I defined a territory as the area associated with a cluster of nests and reoccupancy as a nesting attempt. In most cases reoccupancy was proven by seeing a goshawk in a nest, but in some cases reoccupancy was inferred by detection of new greenery in the nest along with seeing goshawks nearby, or by finding recent goshawk feathers or egg fragments at the nest. Despite speculation (Kennedy 1997) that some of the located territories might originally have been occupied by other species, goshawks were seen on nests in 97% of the studied territories, while the single remaining nest cluster was presumed to belong to goshawks due to nest and stand characteristics plus goshawk activity near the nest.

Nests were located within timber sale assessment areas chosen by foresters: areas which I termed “locales.” Timber sale preparation involved assessing every individual tree over roughly 83% of each locale, including all trees in nearly 100% of the stands suitable for goshawk nesting (described by Crocker-Bedford and Chaney 1988), so there was a high likelihood of finding at least one of the nests of a territory. Once a nest was located, the vicinity was extensively searched for alternate nests.

Harvests of dead and dying trees occurred almost everywhere in my study area from 1945–70. Control locales ($N = 9$; the smallest contiguous block was 4700 ha) did not incur timber sale harvest from 1970 until after nest monitoring was completed in 1987. Treatment locales ($N = 6$; the smallest contiguous block was 1000 ha) were harvested after treatment territories were located but before 1985. Nineteen control territories (nest clusters) were located within the control locales, while 12 treatment territories were located within the treatment locales. I did not include 40 other goshawk territories known by 1987 because they did not fit the above criteria. Partial harvests and selection harvests, not clearcuts, removed about one-third (range = 15–50%) of the sawtimber volume from about 79% (range = 73–86%) of the hectares in treatment locales. No-cut buffers were left around goshawk nests (small buffers were 1–3 ha; large buffers were 16–200 ha).

One strength of my study was that I demonstrated long-term nest-tree fidelity in the absence of habitat degradation. For individual nest trees in control locales, reoccupancy at least once in 1985–87 was equal between nests found in 1973–78 (67%) and those found in 1981–84 (65%). Despite no-cut nest buffers, I found that the average reoccupancy rate from 1985–87 in treatment locales was only 20–25% the rate in control locales. In 1987, the two nests occupied after treatment (occupied treatment nests) had zero and one nestling, while the 12 occupied control nests averaged 2.1 nestlings. No-cut nest buffers were similarly ineffective, whether small or large. Prior to the publication of my results, goshawk

management recommendations concentrated on nesting habitat (Reynolds et al. 1982, Crocker-Bedford and Chaney 1988, Kennedy 1988). After my paper was published, the critical importance of hunting habitat throughout the home range was recognized (Crocker-Bedford 1990, Warren et al. 1990, Reynolds et al. 1992). The differences in breeding and reproduction between treatment and control locales were consistent with the extent of the timber harvests as well as literature showing that mature forest with denser than average canopy is the most selected foraging habitat (Widen 1989, Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994, Iverson et al. 1996, Beier and Drennan 1997).

These results were consistent with results I reported for the same study area (Crocker-Bedford 1987, Crocker-Bedford 1995). In the 1987 paper, I considered only nests known to be occupied in 1982–83, and compared their reoccupancy in 1984–85 according to whether logging occurred after they were occupied in 1982 or 1983. In the 1995 paper, I analyzed 1987 reoccupancy and reproduction from a larger number of territories ($N = 53$) in relation to the amount of timber harvest during 1973–86 within circles of 2.7-km radius around the center of each nest cluster.

Breeding population projections, based on results from my studies, were consistent with a nearly complete census of the study area made by Reynolds and Joy (1998). Given the reduced reoccupancy in logged locales, along with the amount of habitat logged, I (Crocker-Bedford 1990) estimated that by 1988 nesting pairs were probably reduced to half the 1972 breeding population. In the 1990 paper, I only considered breeding density surveys through 1985 because they had already been published (Crocker-Bedford and Chaney 1988). However, by 1987 I had goshawk survey data from six tracts totaling 270 km² which had not been harvested since 1970, and which averaged a breeding pair density of 12 or 13 pair per 100 km² (Crocker-Bedford unpubl data). Given 1200 km² within the breeding range of goshawks on the North Kaibab Ranger District, about 150 pairs may have existed circa 1972. If half were lost by 1988, the remaining breeding population would have been about 75 pairs. Data presented by Reynolds and Joy (1998) demonstrate that the comparable figure was somewhere between 49 and 73 pr during 1991–96. From a census of 95% of the goshawk habitat on North Kaibab Ranger District, Reynolds and Joy (1998) reported that 95 territories were occupied at least once between 1991–96, so about 100 territories remained on the District. Their mean annual rate of occupancy (defined as at least one goshawk seen at least twice within a territory; not necessarily a nest attempt as in my studies) was 73%. Whereas 100% of my occupied control territories produced young, only 67% (range = 44–92%) of the occupied territories produced young in 1991–96 or, in other words, an average of only 49 pairs were successful from 1991–96.

My results also showed changes in the raptor community associated with treatment territories. While I never found another raptor nesting within 1 km of any control nest, other raptor species used nests or nesting stands formerly occupied by goshawks in seven of 12 treatment territories.

Comparisons of my 1990 paper involved the same years, and control and treatment locales were well distributed over the study area. As a result, comparisons were less likely to be confounded by factors such as weather conditions (Penteriani 1997), prey cycles (Doyle and Smith 1994), and inherent site productivity; these can confound correlations between demographic statistics and habitat differences over time.

My study was not biased by an inappropriate or inadequate nest search effort. The number of nest trees known per territory was the same for reoccupied controls (2.33), unoccupied controls (2.25), reoccupied treatments (2.33), and unoccupied treatments (2.44), which demonstrates that search effort was appropriately balanced. Furthermore, I reported the largest number of goshawk territories (71) and nest trees (157) of any published paper through 1990. Thirty-one of the territories, including 73 known nest trees, met the criteria for inclusion in my analyses, yielding the largest sample size of any study by 1990 on *A. g. atricapillus*. The differences between treatment and control locales were highly significant in terms of goshawk reoccupancy ($P = 0.001, 0.003$ and 0.01), number of nestlings ($P = 0.003$ and 0.001), and use by other raptor species ($P < 0.001$).

Despite its strengths, there were also several weaknesses in my 1990 paper. The difference between the number of nestlings found in occupied treatment and control territories may have been due to sample size. Few nests were occupied in treatment locales. As in almost all raptor research, my studied territories were neither randomly selected nor randomly assigned as treatments or controls. Therefore, the results should be considered correlative and not a true hypothesis test for cause and effect relationships.

Perhaps most importantly, the study was not designed to assess effects at the population level. In 1982, I was directed to compare the efficacy of small and large no-cut nest buffers for maintaining goshawk nest site usefulness. The 1990 paper should have explicitly stated implicit assumptions regarding estimates of population change. Despite no-cut nest buffers, some goshawks which had been nesting in the treatment locales before logging might have moved to unlogged areas for nesting. If so, the total nesting population may have been stable. Also, if breeders packed into unlogged areas, then surveys of pair density prior to treatment may have been artificially high. Moreover, the estimate of the size of the breeding population prior to any significant logging (circa 1945) was likely flawed, in that it was an extrapolation based on densities in the two locales harvested the least prior to goshawk surveys. The locales were too few and

too small (1000 ha and 2750 ha) to provide a reliable estimate.

Some of my study's results may have been temporary. The 1990 paper discussed how forest birds and tree squirrels (*Sciurus aberti* and *Tamiasciurus hudsonicus*) were reduced in numbers by selection harvests. However, I did not consider that other species might eventually increase in the more open forest, so that prey composition might shift (Boal and Mannan 1994).

COMMENTS ON KENNEDY (1997)

A species may be listed as Threatened or Endangered under the ESA due to any one of five criteria (United States Government 1988). Kennedy (1997) only dealt with the range contraction portion of one of these criteria, the present or threatened destruction, modification, or curtailment of its habitat or range (United States Government 1988).

Kennedy provided a literature review that, for the eastern U.S., showed that goshawks there were reduced in abundance during the 19th century and, since 1950, goshawk abundance has increased and the species' range has apparently expanded, logically due to reoccupancy as forested landscapes have increased and matured following the extensive deforestation of the 19th century. Perhaps she thought it obvious, but she should have explicitly stated that goshawks can be reduced in number and apparently even extirpated in landscapes where timber harvesting is too great, and that for most of western North America extensive timber harvesting did not begin until the 20th century.

Kennedy (1997) went to great lengths to present demographic statistics related to the rate of population change (λ). However, except in situations where the rate of population change is far different from neutral ($\lambda = 1.0$), it is usually impossible to calculate a meaningful λ for a sparsely distributed species. The number of samples, needed by each age class to calculate rates of pairing, natality, survival, emigration, and immigration, are typically so few from a sparsely distributed species that the calculated λ shows a confidence interval ranging from population increase to population decrease.

Demographic statistics generated from goshawk studies have additional problems. Some results vary with prey cycles (Doyle and Smith 1994) and weather (Penteriani 1997). Immigration and emigration may also vary (Squires and Reynolds 1997) and are affected by the degree of population isolation. DeStefano et al. (1994) describe problems associated with marking and resighting goshawks at nests, such as potentially underestimating survival. Maguire and Call (1993) determined that a λ based on data from existing goshawk nest sites can be biased high, so that a declining trend in habitat carrying capacity, where 1% is lost each year, produces certain extinction in populations whose growth rates are otherwise stable or increasing.

Reynolds and Joy (1998) could not determine λ ,

though their study is so far the most intensive in North America on goshawk demography. Also, they held the advantage of starting with a large number of territories (known from the work of Crocker-Bedford 1990 and Zinn and Tibbitts 1990). In addition, because the study was conducted in one of the most isolated tracts of goshawk habitat, it should have been less affected by immigration and emigration. Since Reynolds and Joy's (1998) intensive and exacting demographic study could not determine λ for a relatively discrete and small study area, it is unlikely that sufficient technology and funding exist to determine whether regional populations are increasing, stable, or decreasing. Moreover, due to effects of weather and prey cycles, demographic data collected during one time period might have little relevance to another.

Kennedy proposed overcoming sample-size problems by pooling published and unpublished goshawk data into a metaanalysis. However, even a metaanalysis is unlikely to overcome the problems described above to a degree that would yield a rate of population change meaningful for a status review (i.e., a λ with a small confidence interval which is applicable over the long-term and an entire region). Furthermore, demographic data are not collected or stored by a consistent protocol. Finally, because the areas where goshawks have been studied have not been randomly selected and because some landscapes are probably population sources while others are likely population sinks, combining studies will not likely represent the true mean of a region.

These problems may explain why the U.S. Congress did not include a documented population decline as a criterion for listing a species under the ESA (United States Government 1988). Some scientists (e.g., Braun et al. 1996, Kennedy 1997) seem to believe that results from demographic studies should prove that goshawks are decreasing over a large portion of their range before the species is entitled to special management. However, I suggest that some scientists may be so involved with demographic data and statistical analyses as to occasionally overlook the importance of deductive reasoning in management.

Kennedy also used unpublished demographic data from her goshawk studies, an approach which was inconsistent with her determination to not include results from non-peer-reviewed literature. Given her standard for others, I would have expected to see her studies peer-reviewed and published separately before appearing as summaries in her 1997 paper. Her presentation of unpublished studies was so brief that the quality of the methods, data and analyses, and appropriateness of the conclusions and inferences, could not be evaluated. For example, the increase in the number of territories found over the first five years of the Ashley study likely was meaningless with respect to population change. Moreover, three of the marked populations described by Kennedy have had little or no habitat modifications within

about 90% of individual goshawk territories since the individual demographic studies began (Desimone 1997); therefore, it is not surprising that the studies did not provide evidence of population decline. Kennedy did not cite several agency reports that indicated reduced nest occupancy or reproduction, even though these had undergone more peer review than her demographic analyses (Bloom et al. 1985, Patla 1991, Ward et al. 1992, Arizona Game and Fish Department 1993, Maguire and Call 1993, Patla and Trost 1995).

She also neglected the extensive literature on the habitat relationships of goshawks, even though such literature is critical for evaluating the amount of habitat destruction or modification, a key listing criterion of the ESA (United States Government 1988). Goshawks apparently prefer stands of relatively large trees with relatively dense canopies for nesting and foraging (Moore and Henny 1983, Speiser and Bosakowski 1987, Crocker-Bedford and Chaney 1988, Widen 1989, Austin 1993, Bright-Smith and Mannan 1994, Hargis et al. 1994, Iverson et al. 1996, Beier and Drennan 1997). Typically, they select larger stands or less-fragmented landscapes (Bent 1937, Widen 1989, Speiser and Bosakowski 1987, Falk 1990, Bosakowski and Speiser 1994, Bright-Smith and Mannan 1994, Woodbridge and Detrich 1994), though some nesting stands are surrounded by areas that are naturally treeless (Swem and Adams 1992, Younk and Bechard 1994).

One purpose of the ESA is to provide a means whereby the ecosystems upon which Threatened and Endangered Species depend may be conserved (United States Government 1988, Sec. 2[b]). Ecosystem conservation may be one reason why any species, or any distinct population segment of any species (United States Government 1988, Sec. 3[15]), needs to be likely to become an Endangered Species within the foreseeable future in only a significant portion of its range (United States Government 1988, Sec. 3[19]) in order for the entire species or segment to be listed. What constitutes a significant portion of its range is debatable for the Northern Goshawk or the population segment west of the Great Plains. Because the goshawk is an indicator of ecosystem health (a predator of forest birds and medium-sized mammals), I would be concerned if its abundance was seriously declining in areas far smaller than during the 19th century in the eastern U.S. For the Northern Goshawk, I suggest that 100 000 km² is significant where forest cover once dominated the landscape, while a disjunct forest as small as 1000 km² might also be significant under the concepts of the ESA.

Kennedy concluded, "Although the concerns about overharvest of forested communities is certainly justifiable, listing a species for which there is no evidence of a population decline would be a misuse of [ESA] legislation." The ESA does not require evidence of population decline. Moreover, if concerns about overharvest of forested communities are justifiable, then this assertion by Kennedy supports one of her alternative conclusions that

"it is possible the goshawk is declining and the decline is going undetected because of the paucity of data on temporal trends in mortality and abundance." If forests in some regions are being harvested faster than goshawk habitat is developing, then goshawks in those regions will be impacted long before demographic analyses indicate problems such as those described by Widen (1997).

Kennedy did not fully report the data from my publications. The correct figure from Crocker-Bedford and Chaney (1988) for the number of nests studied was 74. Kennedy shows a question mark instead of the data. It appears that she might have intended the *N* in her Table 1 to be number of occupied nests. If so, then the correct figure for Crocker-Bedford and Chaney (1988) was 24 because the average occupancy rate of nests was 33%. She defined nest success as the proportion of occupied territories that produce at least one young of bandable age. She reported the figure as unavailable in Crocker-Bedford (1990). In fact, I reported 1.00 for occupied control territories and 0.50 for occupied treatment territories.

A HABITAT-BASED STATUS REVIEW

Kennedy concluded that a detailed analysis of 20th century deforestation and reforestation rates throughout North America would provide additional indirect information on potential temporal changes in the goshawk's range. I strongly support this recommendation. However, because reforestation generally refers to development of seedlings and saplings, I recommend analyzing forest maturation rates in order to emphasize habitat useful to goshawks.

In addition, for each North American region and forest type, goshawk habitat requirements should be estimated at three scales: the amounts of important habitats necessary to support a productive breeding pair; the composition within a landscape for a stable or increasing local population; and the composition within a region for a stable or increasing regional population. To estimate the habitat requirements, a committee of goshawk experts should be convened. These experts should represent diverse views and different regions. The committee should be chaired by a scientist who has not been influenced by the North American goshawk debates. Although the chairperson should be a strong facilitator of group consensus, the committee report should present alternative hypotheses.

Goshawks tend to hunt in mature forests, especially larger stands with relatively dense canopies, and goshawks are more likely to kill prey in mature forests. Nevertheless, goshawks may successfully forage in some open habitats (Kenward 1982, Reynolds et al. 1992, Swem and Adams 1992, Younk and Bechard 1994). This dichotomy is part of the current philosophical debate over whether management of publicly-owned forests should emphasize timber production, or emphasize pristine conditions including many stands of old trees and large tracts left to

nature. Even if a silviculture system can produce both timber and goshawks, some people question whether it is appropriate for wildlife on publicly-owned wildlands. Managers of public forests address such questions as they implement laws passed by elected politicians. To provide information for both philosophies, the committee of diverse goshawk experts should address management by silviculture to develop adequate habitat within a forest scheduled for logging, as well as management by habitat reserves including the sizes, shapes, structures, and spacings of old stands and large tracts to be left unharvested in perpetuity.

I hypothesize that home ranges are larger and territories are more widely spaced in landscapes where less area exists in stands useful for foraging. Kenward (1982) reported that home range size of goshawks varied to encompass a sufficient amount of prime foraging habitat. Breeding season home ranges typically vary from 6 to 35 km² (Squires and Reynolds 1997), although one adult in California ranged over 69 km² (Austin 1993) and two in Alaska each covered more than 600 km² (Iverson et al. 1996). Breeding pair density varies by an order of magnitude (Squires and Reynolds 1997).

Breeding pair density may depend on the amount of habitat where suitable prey is more abundant than some threshold and is accessible enough (forest structure) that the chance of prey capture in the habitat is worth the time and energy expended. This hypothesis is based on evidence from studies of habitat selection and home range sizes (Kenward 1982, Widen 1989, Falk 1990, Austin 1993, Bosakowski and Speiser 1994, Bright-Smith and Mannan 1994, Hargis et al. 1994, Iverson et al. 1996, Beier and Drennan 1997), as well as deductive logic. Goshawk home ranges would be smaller if goshawks were able to benefit from the total biomass of all the prey species within most habitats. The time for hunting is likely inadequate for goshawks to directly assess prey abundance and accessibility in every hectare of their large home ranges, so goshawks need search images for habitats that are likely to be useful. Furthermore, selection harvesting 10–39% of the area within home ranges had no apparent effect on reproduction in half the cases, while in the other half goshawk nesting seemed to be eliminated (Crocker-Bedford 1995), and I suspect this difference was due to whether harvesting occurred in important foraging habitats. Finally, even selection harvesting has the potential to degrade habitat below some threshold of usefulness, and it can reduce forest prey populations (Crocker-Bedford 1990).

I hypothesize that most forest structures and most area within the typical home range provide little or no benefit to goshawks. Consequently, timber operations that miss important habitats may have little or no effect on home range size or breeding density. However, timber harvests in important foraging habitat likely have effects disproportionate to their sizes.

CONCLUSIONS

Goshawk demographic trend studies typically require decades of data collection to be useful for population status assessment (Widen 1997). Even then, anyone who wishes to doubt the long-term results could assert that any trends found were really due to weather, prey cycles, inconsistent techniques, or inadequate sampling. Rates of population change (λ) for goshawks are also open to question owing to wide confidence intervals, inherently biased field techniques, and data representing few years and a small number of nonrandom study sites. Environmental degradation could continue for many years or decades while demographic data are collected, and habitat degradation might continue as litigants and their consultants debate whether the trend data or λ statistic are meaningful.

Studies comparing goshawk parameters in relation to forest management practices are unlikely to ever achieve all criteria of ideal experimental designs for hypothesis testing. No landowner will ever dedicate to goshawk research multiple large tracts of forest ($>1000 \text{ km}^2$), nor is there likely to be adequate financing and enough time to locate most goshawks before the experimental treatment, gather pretreatment data, perform manipulations in randomly selected home ranges, wait for the manipulations to have their habitat effects, and then gather the comparison data. Still, comparison studies that fall short of the perfect experimental design will typically have fewer problems with confounding factors than will long-term trend studies of forest management effects.

Goshawk research that is funded to gather information for management purposes should compare goshawk parameters (e.g., demographic data, home range sizes, spacing of territories, habitat selection, diets) between replicates of similar landscapes under different management treatments. Whenever possible, data should be collected before treatment to demonstrate the pretreatment similarity of the landscapes with respect to the parameters studied. Retrospective studies allow more rapid insights into management questions at lower costs, and aerial photos can suggest pretreatment similarity (Ward et al. 1992).

Because replicates of management treatments and controls are unlikely to ever be randomly assigned to areas large enough to fully encompass home ranges, scientists should explicitly recognize that goshawk field studies are correlative, and should not interpret their results as absolute proofs. Nevertheless, they should not be dissuaded from providing logical deductions based on data and literature, although they should also explicitly state their assumptions.

Goshawk experts from different regions, including proponents of divergent theories, should be brought together to consider landscape-level habitat requirements. After gathering information from forest inventory experts on forest-landscape changes, the team could assess

whether goshawks in portions of the U.S. deserve protection under the ESA, which does not require habitat threats to be range-wide before listing a species or population segment. I hypothesize that goshawks are supported by only a portion of the habitats present, and that typically most of a home range (especially where trees are small or sparse) provides little or no sustenance to individuals.

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EVALUATING NORTHERN GOSHAWK (*ACCIPIITER GENTILIS ATRICAPILLUS*) POPULATION STATUS: A REPLY TO SMALLWOOD AND CROCKER-BEDFORD

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Shawn Smallwood and Cole Crocker-Bedford present thought-provoking reviews of my recent paper on Northern Goshawk (*Accipiter gentilis atricapillus*) population trends (Kennedy 1997). In addition, Crocker-Bedford provides a detailed review of his controversial 1990 paper on forest management and its impact on goshawk reproduction (Crocker-Bedford 1990). Finally, both authors present their ideas on alternative approaches that might be used to evaluate the status of the goshawk. Here is my reply to their comments.

OBJECTIVE OF KENNEDY (1997)

Smallwood and Crocker-Bedford find fault with my paper because I did not include habitat analyses. They rightly claim that evaluating habitat loss is a key listing criterion of the Endangered Species Act (ESA). I do not disagree with them and think a thorough analysis of goshawk habitat data is an important component of a status review. But the aim of my paper was not to conduct a status evaluation for the listing proposal, which was clearly misunderstood by the two authors. A status review is the purview of the U.S. Fish & Wildlife Service (USFWS) and they just finished such an evaluation (Clark 1998). I merely evaluated the petitioners' claim "that goshawk populations have suffered significant declines." I wanted to see if the statements presented by the petitioners as fact indeed had empirical basis. I treated their statement as an hypothesis, proceeded to test this hypothesis, and found no support for their statements.

The goal of my paper was to conduct the first step in a status assessment and determine, in a scientifically thorough manner, if there is evidence of a population decline. I did not continue to the next step, that of determining reasons for a decline, because, as I stated in my paper, "Diagnosing a cause of decline is irrelevant if there is no evidence that a decline has occurred." Once some evidence of a decline has been documented then the cause(s) of the decline can be determined and appropriate conservation plans developed and implemented (Caughey and Gunn 1995). If there is no evidence of a demographic decline, how can we justify spending taxpayer dollars to develop and implement expensive recovery programs? Without demographic data, how does the recovery team establish achievable, quantifiable recovery goals as delisting criteria (see Pagel et al. 1996, Cade et al. 1997, and Pagel and Bell 1997 on the debate about recovery goals for American Peregrine Falcons [*Falco peregrinus anatum*])? The USFWS used a similar approach in their recent status evaluation where they examined evidence that goshawk populations were declining and then proceeded to evaluate the potential loss of goshawk habitat. They concluded that listing the goshawk as Endangered or Threatened west of the 100th meridian is not warranted (Clark 1998).

WHAT RESPONSE VARIABLES ARE APPROPRIATE TO EVALUATE GOSHAWK POPULATION TRENDS?

Evaluating Goshawk Trends Using Demographic Variables. There are two general approaches that can be used

to monitor population trends: the survey method and the demographic method (Taylor and Gerrodette 1993). Using a survey method would entail attempting to estimate population size (or some index of population size) directly over several years and determine whether or not the estimates indicate a decline over time. Because it is not feasible to census the entire population of most bird species (including raptors), population monitoring is almost always based upon surveys of a sample of the population. The demographic method involves monitoring trends in vital rates (survival, fecundity, immigration, and emigration) and then using these data to calculate finite population growth rate (λ). λ can be calculated by following reproduction and survival of individual cohorts (age classes), or it can be estimated through simulation based on annual variation in cohort survivorship and reproduction (Gotelli 1998).

In my paper, I examined available data that could be used to monitor goshawk population trends, using either the survey or demographic approach. Surprisingly, neither author thought any of the demographic response variables I chose to evaluate trends was useful for determining goshawk population status! In his conclusions, Smallwood states: "Population density, fecundity, survival and rate of population change all lack scientifically defensible relationships with range-wide abundance. . . ." I disagree and still adhere to the basic tenets of population biology that I describe here. Attaining accurate measurements of these parameters that are appropriate for the scale of inference, however, is problematic but not impossible.

Population Abundance. Abundance refers to the number of individuals within a population (or population size) (Krebs 1994). If the population is so large that a study cannot encompass the whole of it (e.g., range-wide goshawk population), then abundance must be presented in terms of densities rather than absolute numbers. Thus samples are taken and abundance is expressed as number of animals per unit area (Begon and Mortimer 1986). Density is thus the spatial expression of abundance (Krebs 1994). Temporal trends of density would reflect temporal trends in abundance. As indicated by Smallwood, simple tallies of nests to estimate breeding density in a study area is fraught with problems and produces biased estimates of population size (Gould and Fuller 1995). Rather than rejecting density as an appropriate response variable, this problem could be solved by estimating population size using Jolly-Seber models. The Jolly-Seber model is a capture-recapture model allowing for an open population in which additions and/or deletions occur. The model produces population density estimates for each sampling period (e.g., year). This method has been described extensively in the literature and the application of this approach to raptors is described in an excellent paper by Gould and Fuller (1995).

Another potential approach for monitoring abundance of goshawks is the area-occupied technique (Iver-

son and Fuller 1991). This approach employs repeatedly broadcasting calls from the same locations, and using the pattern of responses to estimate the probability of detecting an animal given that one is present. Probability of detection—area occupied techniques have been used successfully on another woodland raptor, the Red-shouldered Hawk (*Buteo lineatus*, McLeod and Andersen in press), and are particularly promising for monitoring species in landscapes where proportion of area occupied is high, and birds have a high probability of responding to a call. To date, little work with this technique has been conducted with goshawks. However, goshawks respond to call broadcasts (Kennedy and Stahlecker 1993); thus, this approach may be useful in monitoring their populations.

Before this technique could be applied widely, it would need to be validated in areas where goshawk density has been estimated independently. Currently, the relationship between estimates of area occupied and breeding density have not been clearly established; so, before this technique could be used to monitor breeding density, such a relationship would have to be evaluated. Bart and Robson (1995) describe a double-sampling procedure that could be used to calibrate this technique. Density could be estimated on quadrats using foot (Rosenfield et al. 1998) or aerial surveys for occupied nests (aerial surveys could only be used before leaf-out in deciduous habitat [see Cook and Anderson 1990 for an example]). These estimates would be compared to the estimates obtained from the area-occupied technique and the area-occupied estimates would be adjusted accordingly.

Vital Rates. The population attributes (or vital rates) influencing changes in abundance are immigration and birth, which increase abundance, and emigration and death which reduce it (Begon and Mortimer 1986, Krebs 1994). The combined effect of these four processes provides an accurate indication of how abundance changes. λ potentially can be estimated with a high degree of precision and accuracy. Both authors criticize the use of these demographic variables because of sampling difficulties. Crocker-Bedford states that "... it is usually impossible to calculate a meaningful λ for a sparsely distributed species." This is not true. Meaningful λ s have been calculated for several species of management concern including the Northern Spotted Owl (*Strix occidentalis caurina*, Burnham et al. 1996) and Ashy Storm-petrel (*Oceanodroma homochroa*, Sydeman et al. 1998). I agree with Crocker-Bedford that this parameter is difficult to estimate particularly when using capture-recapture data to estimate survival. However, survival rates can be determined using other methods such as radiotelemetry (Iverson et al. 1996, Ward and Kennedy 1996, Ganey et al. 1998). The estimation procedure is less complex than for banding data (see White and Garrott 1990) and I hypothesize that smaller sample sizes would be required than with capture-recapture data, although I have not conducted a power analysis to test that hypothesis.

Contrary to the criticisms of both authors, I still think

a metaanalysis would be useful to estimate goshawk fecundity and survival from currently available vital rate data collected at individual study areas. This approach was used successfully to analyze Northern Spotted Owl datasets (Burnham et al. 1996) so there is no reason why this approach could not be used for the goshawk which is a species that is more widely distributed and probably more abundant than the Northern Spotted Owl. This metaanalysis would be an inexpensive next step to determine what types of data are needed and how many study areas would be required to obtain sufficient data. For example, using this approach, the datasets of Reynolds and Joy (1998) referred to by Crocker-Bedford could be pooled with the survival data presented in my paper and in DeStefano et al. (1994). Because sampling protocols were similar in all three study areas, survival estimates could be analyzed for the years in which the studies overlapped (1991–92 for all three studies and 1991–95 for New Mexico and Arizona). This should be done before more resources are committed to collecting vital rate data and the results of the analyses could be used to assist the design of future long-term studies. I agree with Smallwood that a metaanalysis should not be used in lieu of proper sampling. However, it is an underutilized tool that can be used to analyze data from multiple, well-designed, coordinated studies which are unlikely to estimate population trends individually due to the rarity of the species.

Evaluating Goshawk Trends Using Migration Counts. Smallwood suggests that goshawk abundance should be evaluated based on changes in migratory counts. The utility of migration counts for monitoring population trends has been much debated (see Bildstein 1998 for a detailed discussion of the strengths and weaknesses of migration counts as an index to population size). To track population change, a constant proportion of the index (e.g., migration counts of goshawks) to the true population size must be maintained. If this does not occur then the proportion must be estimated. These validation studies have not been conducted on the goshawk for a local area or range wide, so the trends in the current migration count data are difficult to interpret.

Also, trends in migration counts could reflect distributional changes or changes in residency patterns rather than changes in population size. For example, recent analyses of Christmas Bird Count data suggest that Sharp-shinned Hawks (*A. striatus*) are increasing. Several authors have suggested that more Sharp-shinned Hawks are overwintering in northern North America because of warmer winter climates and/or the abundance of bird feeders which provide a stable overwinter food source (see review in Bildstein 1998). This could be the reason that counts of Sharp-shinned Hawks at northern migration stations have been lower in recent years. Since goshawk migrations are characterized by irruptive invasions, migration counts of this species are more likely to reflect residency patterns than changes in abundance (Bednarz et al. 1990, Titus and Fuller 1990). So, in response to

Smallwood, to replace demographic variables that are known to represent abundance or influence abundance with an uncalibrated index is inappropriate. However, migration counts could be continued and used as an addendum to demographic studies to determine if the counts reflect demographic changes in goshawk populations.

Evaluating Goshawk Status by Monitoring Habitat Variables. What is the role of monitoring habitat variables in determining the status of goshawks? I agree with Smallwood, Crocker-Bedford, and DeStefano that habitat variables should be included in a goshawk-monitoring program. However, as noted by Crocker-Bedford and DeStefano, habitat monitoring should augment demographic studies, not replace them. Evaluating goshawk status purely from migratory counts and information on habitat availability and contiguity as suggested by Smallwood assumes that goshawk habitat can be defined and that the relationship between these variables and goshawk abundance is well-documented. Currently, these relationships are not well-defined.

In the recent status evaluation the USFWS concluded, “The information presented in the petition relies largely on the contention that the Northern Goshawk is dependent on large, unbroken tracts of ‘old-growth’ and mature forest. However, the Service has found no evidence to support this claim. The Service found that while the goshawk typically does use mature forest or larger trees for nesting habitat, it appears to be a forest generalist in terms of the types and ages of forests it will use to meet its life history requirement. Goshawks can use small patches of mature habitat to meet their nesting requirements within a mosaic of habitats of different age classes . . .” (Clark 1998). I concur with their findings and suggest that more habitat studies are needed that are designed to determine the range of habitats used by the goshawk. I agree with Smallwood, Crocker-Bedford, and DeStefano that these studies need to be conducted at multiple spatial scales to be meaningful. I would add that habitat studies should be conducted year-round and not just focused on nesting habitat. Our knowledge of goshawk winter ecology is appallingly scant (Squires and Reynolds 1997). Finally, I concur with DeStefano that trends in forest habitat availability should also be documented to determine trends in availability of goshawk habitat.

Once goshawk habitat is well-defined and demographic data are available from several study areas for an analysis of population trends (see DeStefano for further discussion of the value of long-term studies at multiple study areas), I’d recommend we begin development of a model (or models) that predicts the relationships between suitable nesting and winter habitat and population trends and/or performance. This predictive model will need to be refined and tested to examine relationships between habitat data and population size or other relevant demographic parameter. If a habitat model can predict goshawk population performance, then monitoring pro-

grams can switch emphasis from population-based monitoring to habitat-based monitoring. If habitat models do not adequately predict population performance, population-based monitoring will need to be continued and the habitat relationship information will need to be reevaluated.

This approach is based on ideas presented by recent monitoring plans for the Marbled Murrelet (*Brachyramphus marmoratus*, Madsen et al. in press) and Northern Spotted Owl (Lint et al., in press) in the Pacific Northwest, and monitoring plans for the goshawk in the western Great Lakes region (Kennedy and Anderson unpubl. data). The emphasis is to use the demographic and habitat data collected in the initial phases (Phase I) of a monitoring program and to develop habitat-based models that use habitat features to predict goshawk occurrence and demographic performance in the latter phases (Phase II) of a monitoring program. If reliable habitat models can be developed to predict population status and trend at a landscape scale, monitoring can switch from intensive and costly population-based monitoring to a less expensive habitat-based monitoring approach. The habitat-based monitoring would emphasize monitoring the habitat features that predict goshawk performance and/or status, with less emphasis on monitoring population parameters. However, presence/absence of breeding goshawks in suitable habitat (as identified by the habitat models) would need to continue in Phase II to ensure that this habitat remains occupied. I emphasize that the switch from Phase I to Phase II can only occur if the habitat models are demonstrated to reliably predict goshawk population performance. Models that are not validated are essentially equivalent to untested hypotheses, so population-based monitoring would have to continue until validated models are developed.

In addition to the model development, I strongly support DeStefano's suggestion that on-site experiments designed to measure goshawk responses to silvicultural treatments be initiated. These quasi-experiments are being implemented continuously in the form of timber harvest near goshawk nests; most sale areas are identified years before the sale allowing for the collection of adequate pretreatment data. Monitoring pre- and posttreatment movements of even a few pairs of birds would provide us with fascinating qualitative insights into goshawk responses to harvest and could be the basis for designing additional experiments.

Crocker-Bedford does not think field experiments like this are possible and states, "Scientists should explicitly recognize that goshawk field studies are correlative. . ." I disagree with this statement because these types of landscape-level, quasi-experiments have been conducted on passerine communities (Bierregaard and Lovejoy 1989, Schmiegelow et al. 1997) and goshawks have been successfully used as experimental units in field experiments (Kenward et al. 1993, Ward and Kennedy 1996, Dewey 1998). Thus, we are not restricted to correlative studies.

Although correlative studies are valuable in identifying patterns, they do not imply cause and effect (Romesburg 1981, 1989, Krebs 1994). For example, trends in population or habitat availability do not imply causes of population change; experimental data are needed for such an evaluation. Raptor biology can move beyond its dependence on the correlative approach and toward more field experimentation with creative thinking about how to test hypotheses and a willingness to try new approaches. Romesburg (1981) claimed nearly two decades ago that much wildlife science was compromised with respect to providing the reliable knowledge required to make management decisions. He argued that management should be based on "good science," which is the scientific evidence best able to provide reliable knowledge. Reliable knowledge is based on the hypothetico-deductive (H-D) method. The H-D method employs three steps: observation/induction, hypothesis formation and experimentation (Romesburg 1981, 1989). Crocker-Bedford is arguing that we approach goshawk management by only completing the first two steps. What typically happens when this is done in management is hypotheses advanced to account for observations gradually evolve into explanations for them through a process Romesburg (1981) called retrodiction. The petitioners' statements about goshawk declines are examples of retrodiction.

COMMENTS ON CROCKER-BEDFORD (1990)

In addition to providing a thoughtful critique of my paper, Crocker-Bedford dedicates a considerable segment of his rebuttal detailing methodologies and strengths and weaknesses of his controversial 1990 paper. He is providing these details to rebut recent scientific evaluations of his 1990 paper (Kennedy 1997, White and Kiff 1998). Crocker-Bedford's identification of the strengths and weaknesses of his 1990 paper adds a valuable component to this scientific debate and an appropriate addendum to his 1990 paper. However, I disagree with several points he makes.

As I mentioned in my paper (Kennedy 1997), one of the major strengths of Crocker-Bedford's 1990 paper was that it was the first published paper to suggest that goshawk populations were declining due to overharvest of their forested nesting habitat. This idea was important and it fueled this stimulating debate on goshawks and forest management. However, his paper has some serious flaws. Crocker-Bedford implies that his study was criticized because he had conclusions that were politically sensitive. It is likely that some of the unpublished criticisms he received over the years were politically motivated, yet the aforementioned published critiques were based on scientific merit.

Crocker-Bedford claims that one of the strengths of his paper is that he ". . . demonstrated long-term nest tree fidelity in the absence of habitat degradation." Whether or not he demonstrated this depended on his methods for estimating locale reoccupancy, which have still not

been adequately explained. Comparisons of occupancy rates need to be done cautiously because occupancy rate is a subjective parameter that is probably correlated with the amount of effort expended to determine territory status (White et al. 1995, Kennedy 1997). We still do not know if Crocker-Bedford (1990) used standard search effort techniques for treatment and control locales. He states that his study was not biased by an inappropriate nest search effort and justifies this based on his large sample size. However, sample size is not the major factor influencing estimation of occupancy rates, it is search effort. He states "... the vicinity was extensively searched for alternate nests." Was each nest site searched with equal effort and was an equal-sized area searched prior to determining a site was unoccupied? This is important because there is a high probability of missing alternative nests in goshawk territories due to large inter-alternative distances. In California, mean distance between alternative nests was 273 m and the range was 30–2066 m (Woodbridge and Detrich 1994). In Arizona, mean inter-alternative nest distance was 489 m and the range was 21–3410 m. Approximately 89% of alternative nests in Arizona were within 900 m and 95% were within 1400 m of one another (Reynolds and Joy 1998). Clearly, the potential for misclassifying an occupied territory as unoccupied is great if nest site searches are restricted to the immediate vicinity (50–100 m) of the most recently used nest. So small search areas, even if they are consistently applied to treatment and control locales, might result in more false negatives in treatment locales because harvest might influence inter-alternative distances rather than occupancy rates.

The most controversial statement in Crocker-Bedford (1990) was his claim in his summary that the goshawk population on the North Kaibab Ranger District declined, "... from an estimated 260 nesting pairs in 1972 to approximately 60 pairs by 1988." He claims that his breeding population projections are one of the strengths of his paper. I strongly disagree because I think this statement is an example of inappropriate inference given his dataset. He did not provide an analysis of the limitations of his calculations nor did he provide alternative explanations for his results. He based his estimation of rate of population change solely on published breeding density estimates of the areas harvested in the 1950s and 1960s (Crocker-Bedford and Chaney 1988) and his estimates of reoccupancy rates (Crocker-Bedford 1990). He cites unpublished data in this rebuttal that were apparently used in these calculations. However, the methods he used for estimating these densities are unknown and should have been presented in the 1990 paper. In addition, he did not estimate a variance of any of his density estimates, which influences one's interpretation, as I will demonstrate below.

Crocker-Bedford argues that his breeding population projections are corroborated by recent population size estimates of the same area by Reynolds and Joy (1998).

In contrast, I suggest that the Reynolds and Joy (1998) results provide an excellent example of why his projections were an example of inappropriate inference. Reynolds and Joy (1998) estimate that approximately 100 territories currently remain on the District (they have located 95 occupied territories in surveys of 95% of the District). Crocker-Bedford estimated the population size in 1988 to be 60 pairs. If we take a conservative approach and assume the population size has not increased between 1988–96, this suggests that Crocker-Bedford's estimate of 60 pairs could vary by 66% (20–100 pairs). If we extend this simple estimate of variance to his historical estimates they could have varied from 86–432. We cannot compare these ranges statistically because we do not know his estimate of variance, but these calculations suggest that one plausible breeding projection would be that the number of pairs varied between 86–100 between 1972–88, respectively. This is equally as plausible an interpretation as the one provided by Crocker-Bedford (1990).

Crocker-Bedford (1990) used two estimates of density that may or may not be comparable, depending on the estimation procedures, did not provide an estimate of the precision and bias of his estimator, drew a line through these two points, made a single interpretation of the trends and ignored any plausible alternative explanations. This is considered inappropriate inference within the scientific community. Crocker-Bedford (1990) should have concluded that it was not possible to determine if the North Kaibab goshawk population was increasing, decreasing, or stable because of wide variation in demographic estimates. Maguire and Call (1992) reached similar conclusions in their population viability analysis (PVA) for the same goshawk population. They found, "... the range of variability in parameter estimates, particularly for mortality rates, was so great that our simulation results produced populations that ranged from rapidly increasing to rapidly declining. We are unable to conclude from these results whether the North Kaibab Ranger District is stable, increasing or decreasing." Smallwood incorrectly interpreted their study (cited as Maguire 1993) by focusing on the potential for population declines as a result of habitat loss. However, this was not the major conclusion of the Maguire and Call PVA.

CONCLUSIONS

Although neither Crocker-Bedford nor Smallwood can provide empirical results to refute my conclusions or the conclusions of the USFWS status review, their papers provide thoughtful and insightful comments that have stimulated an interesting discussion about approaches for evaluating population trends in goshawks. The disagreement and controversy described by Smallwood and Crocker-Bedford and expanded by DeStefano are characteristics of intellectual ferment driven by the best creative effort of ecologists and are among the reasons why conservation biology and wildlife management are such

exciting fields. I hope these discussions continue and they result in improved approaches to evaluating population trends of rare and uncommon species.

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DETERMINING THE STATUS OF NORTHERN GOSHAWKS IN THE WEST: IS OUR CONCEPTUAL MODEL CORRECT?

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In federal district court in Tucson, Arizona recently, a case was heard regarding the status of the Endangered Cactus Ferruginous Pygmy-owl (*Glaucidium brasilianum cactorum*) and development in the Tucson basin (Defenders of Wildlife vs. Amphitheater School District). The western population (Arizona) of the Cactus Ferruginous Pygmy-owl had been listed in 1997 under the Endangered Species Act (ESA), and a local school district wanted to build on an area allegedly used by one or more

owls. Defenders of Wildlife, as the plaintiff, was suing to stop the development. Owls had been seen just north and south of the boundary of the property in question, and the attorney for the defense built part of her case on the fact that an owl had not actually been seen inside the property boundary. She used this "uncertainty" about the owls' use of the property, as well as other aspects of its little-known ecology in Arizona, to her advantage and stated in court "there comes a point where the

best evidence available isn't good enough" (Nintzel 1998).

That statement is a big problem for biologists in court, and one that could always be used against us. The "best evidence available" will always involve uncertainty because our best data are usually sample data, which, by definition, contain uncertainty (Ramsey and Schafer 1997), and we will rarely have all the data we need. "Uncertainty" is not a negative concept in science, but part of the process (Murphy and Noon 1991, Williams et al. 1996). The courts, however, view uncertainty as equivalent to "a shadow of doubt." If conservationists are always charged with the burden of proof, we will more often than not lose in court, which is where conservation and resource management decisions are made with increasing frequency.

The status of the Cactus Ferruginous Pygmy-owl has implications for a small part of the world—the few parcels of undeveloped land in the unplanned and overdeveloped Tucson basin of southern Arizona. The status of another raptor, the Northern Goshawk (*Accipiter gentilis atricapillus*) has much broader implications. The goshawk is distributed in forested areas throughout much of North America, and the implications of listing this species as Threatened or Endangered under the ESA are far-reaching and important, perhaps even more so than the listing of the Northern Spotted Owl (*Strix occidentalis caurina*) as a Threatened Species in 1990. Like the Northern Spotted Owl, the goshawk is a forest raptor dependent, at least partially, on older forest, and thus millions of dollars worth of timber are involved. This certainly heightens the interest of the public, the Congress, and the courts. In addition, the goshawk occurs over a much broader geographic area than the Northern Spotted Owl. Regardless of the final decision to list or not list the goshawk, court is likely where we are headed.

This paper represents some thoughts on the status of goshawks in the West, including a review of recent events that helped shape the debate over Endangered Species management, a summary of available data on goshawk ecology, some suggestions for additional data that could or should be collected, and some questions on how professional biologists, environmental groups, and society in general invoke and use the ESA. It is also a forum for me to air some of my own uncertainties regarding the status of this species and some suggestions for courses of action for its management and conservation. I hope that any or all of this fosters additional discussion. I focus on goshawks west of the 100th meridian, and refer to this as the West, because that has been the geographic scope of recent listing petitions (U.S. Fish and Wildlife Service 1998b) and includes the area where most of the recent ecological and demographic research has occurred (Block et al. 1994, Kennedy 1997, Squires and Reynolds 1997). Finally, I make liberal use of the pronoun "we" throughout the paper to emphasize the idea that conservation issues are the concern and responsibility of all cit-

izens, and to deemphasize the concept of "us" vs. "them" that so often plagues conservation debates.

A RECENT HISTORICAL PERSPECTIVE

Northern Spotted Owl as Conservation Model. It would be a mistake to evaluate the status of any candidate species for listing under the ESA, and particularly any forest raptor, without first considering the history and implications of the Northern Spotted Owl issue in the Pacific Northwest. Yaffee (1994) called the spotted owl controversy a "watershed event" in resource and environmental policy. In many ways we entered a new era in conservation, with myriad implications in policy, politics, and public relations. Important among them was a stronger focus on ecosystems as the public, through the media, saw the extent of the destruction of old-growth forest (i.e., native forest unaltered by human activities with natural processes [e.g., hydrology, succession, wind-throw, fire] intact). The alteration of ecosystems in North America was not new—consider, for example, wetlands, prairies, and deserts—but the focus and level of attention was something different. Equally important was a demonstration of the power and reach of the ESA. This law became a potent tool for environmentalists; any citizen could petition for a listing (Rohlf 1989), and if listing occurred, there was legal power to alter the rate of resource extraction.

Bridging concerns over the loss of old-growth forests and the power of the ESA to change that trend was perhaps an ideal species: a somewhat mysterious but easily photographed (and thus newsworthy) owl that was an old-growth obligate (Forsman et al. 1984). The listing of the Northern Spotted Owl under the ESA as a Threatened Species brought harvest of old-growth timber in the region to a standstill, an environmental issue to the attention of the nation, and a president to Portland, Oregon for a national meeting. The old growth-Northern Spotted Owl model of controversy, confrontation, and conservation became a template for protection of nature.

A Parallel Course? During the latter stages of the spotted owl issue, Crocker-Bedford (1990) published a paper on goshawk reproduction and forest management in Arizona, citing a correlation between excessive timber harvest and loss of goshawk breeding territories. Petitions to list the goshawk soon followed (Kennedy 1997). At issue again was not only concern for the continued existence of a species, but a desire to stop logging in old-growth forest: not just the mesic forests of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and firs (*Abies* spp.) west of the Cascade Range, but the much more widespread drier forests of Ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and mixed conifers of the interior West. We had just seen a demonstration of the power of the ESA to slow the pace of timber harvest to the benefit of Northern Spotted Owls; perhaps this was the best course for the goshawk.

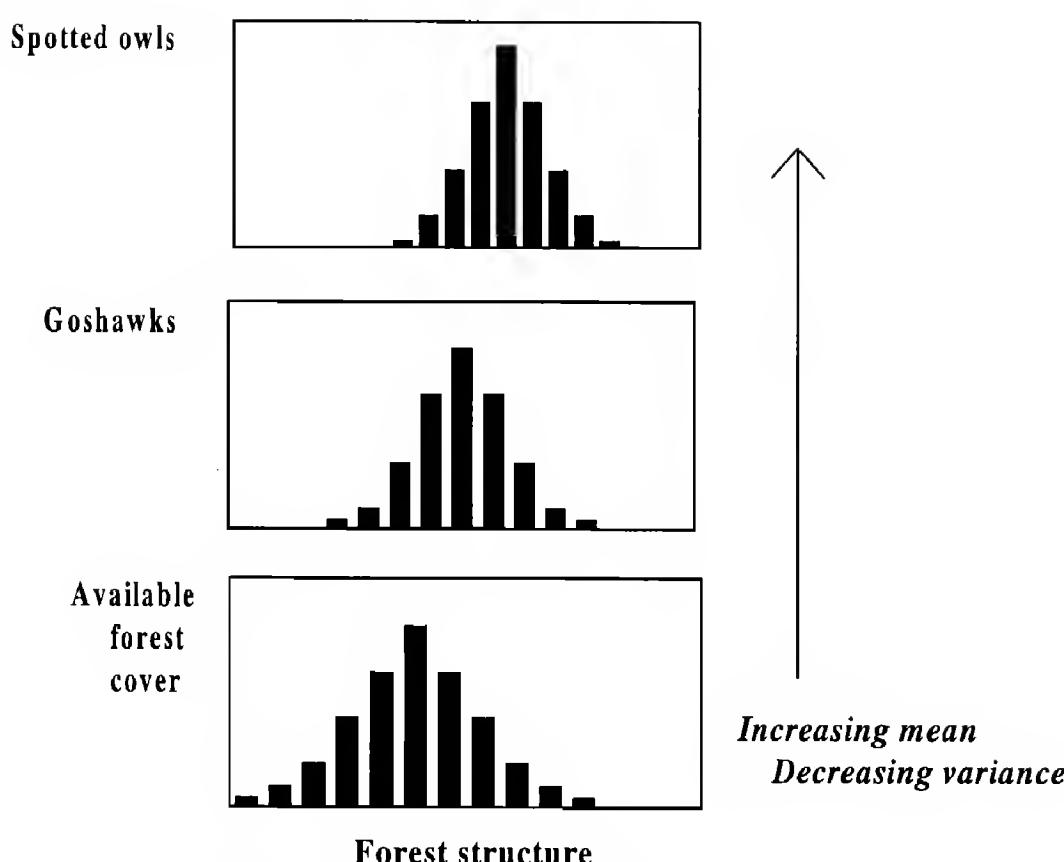


Figure 1. Theoretical graphs comparing Northern Spotted Owl and Northern Goshawk use (e.g., for nest or roost sites) of old-growth forest structure (e.g., density of large trees, high overstory canopy closure) to forest structure available on the landscape. Preponderance of old-growth characteristics increases to the right of the *x*-axis. Northern Goshawks use a wider range of forest structural stages than Northern Spotted Owls, but use older forest more than it is available on the landscape. See text for additional discussion.

GOSHAWKS AND OLD-GROWTH FOREST

Early petitions to list the goshawk prompted a thorough examination of past studies and a host of new studies by independent researchers in several western states (Squires and Reynolds 1997, Daw et al. 1998). Most of these studies focused on nesting habitat, partly because of the importance of breeding biology to the ecology and management of goshawks, but also because it was difficult to approach research on this elusive species in any other way. These studies may be criticized as a duplication of effort, but when one examines them as a group, an interesting and important pattern emerges: goshawks, regardless of region or forest type, tend to select stands with large trees (e.g., >53 cm dbh; Daw et al. 1998) and relatively high canopy closure (e.g., >50–60%; Ward et al. 1992, Daw et al. 1998) for nesting (see Daw et al. 1998 for a summary of research).

I believe it was a combination of our recent experience with Northern Spotted Owls and the pattern of goshawks nesting in forest stands with old-growth characteristics that led many to believe that the goshawk was an “old-growth species.” Reynolds et al. (1992) described what might be optimal goshawk habitat in the southwestern U.S.: it included not only a large percentage of the landscape in older forest, but also a mix of stand types and ages that provides for a variety of prey and takes into account forest stand dynamics (Graham et al. 1994). Importantly, the southwestern management guidelines in-

corporated timber harvest as a mechanism to achieve the desired mix and distribution of forest structural stages.

Fig. 1 illustrates, in a very general way, one idea of how Northern Spotted Owls, goshawks, and forest cover may relate to one another over a broad geographic scale. The *x*-axis can be any forest structure variable or combination of variables that characterize old-growth forest (increasing size of trees, density of large trees, and/or overstory canopy closure); the further right one goes on the *x*-axis the more prevalent are those characteristics. The *y*-axis represents increasing frequency of occurrence; for owls or goshawks it could be number of nest or roosting sites; for available forest cover it is the frequency of occurrence for a particular structural stage on the landscape. Although these graphs are theoretical, data exists to support them (Ripple et al. 1991, Siders and Kennedy 1996, McGrath 1997). The top graph shows that Northern Spotted Owls are found mostly in older forest, with limited variation around the mean, indicating the importance of older forest to their existence. The second graph shows goshawks as being found in a wider variety of forest structural stages compared to spotted owls. Older forest is important to goshawks, but goshawks are more of a forest generalist than are spotted owls. Finally, the third graph illustrates general forest structure across much of the West, based on measurements taken at random points as an index of “availability” (Manly et al. 1993). Compared to the graph for goshawks, the mean is cen-

tered over younger forest and there is wider variance. The relative positions of these three graphs probably would be expected even for pristine forests. Today, however, forests in the West have clearly been forced to earlier structural stages (i.e., forest structure has been "pushed" to the left side of the graph).

The changing structural stage of forests is a trend that should and does concern us. Setting forest succession back through clearcutting old-growth forest west of the Cascade Range has had important implications for Northern Spotted Owls—enough to list the species as Threatened. The effect that multiple entry selective cutting on Ponderosa pine and other dry forest tree species has had on goshawks is also of concern, but the implications are less clear. Given that forest management practices are likely affecting even this relatively versatile forest raptor, the question becomes how to respond to that concern. One possible response is to list the goshawk as an Endangered Species, which would likely stop or at least slow the cutting, as it did for the Northern Spotted Owl. Based on this logic, a series of petitions by environmental groups to list various segments of the goshawk population in the West began in the early 1990s and has continued unsuccessfully well into the decade (U.S. Fish and Wildlife Service 1998b).

THE DATA WE HAVE

Demography. In response to the petitions to list, Kennedy (1997) reviewed the available published literature on the subspecies *A. g. atricapillus* in North America and conducted analyses on demographic data from two populations in New Mexico and Utah. She evaluated the claim that goshawk populations were declining in North America, stating that evidence of a decline would include range contractions, decreases in density, or decreases in fecundity or survival, which might translate into a negative rate of population change (λ). Based on this approach, she concluded that there was no evidence to support the contention that goshawk populations were declining. Importantly, she stated that this result could be interpreted in two ways: goshawk populations are not declining, or goshawk populations are declining but the decline has not been detected. The latter interpretation would be a Type II error and, as such, is of concern to conservation biologists (Steidl et al. 1997).

Kennedy's (1997) review was an important and necessary step in examining the status of goshawks. Cole Crocker-Bedford and Shawn Smallwood have taken issue with Kennedy's approach and have pointed out problems that can arise in collecting and interpreting demographic data. However, demographic information, as difficult as it is to collect, is vital to understanding population dynamics: the available demographic data on any species considered for listing must first be assessed (*sensu* Kennedy 1997) before collection of additional demographic data can be improved (*sensu* Smallwood 1998).

Habitat. Goshawks can be found in a variety of forest

cover types throughout the West (Squires and Reynolds 1997), and in that sense can be viewed as forest generalists. For any given forest cover type, however, goshawks tend to nest in stands with large trees and high canopy closure; their choice of nest sites could relate to microclimate, protection from predation, or something else, but the pattern is well-documented (Daw et al. 1998). Older forest may also be important in the postfledging family area (PFA) (Kennedy et al. 1994, Daw 1997). As one looks at forest cover at increasing distances from the nest, however, older forest becomes less prevalent (Daw 1997, Desimone 1997), and possibly less important (McGrath 1997). While older forest may be less prevalent on the landscape in general because of past timber management activities, older forest away from the nest may be less important to breeding goshawks than older forest immediately around the nest.

Prey. Goshawks hunt in older forest and may even prefer it if it is available (Bright-Smith and Mannan 1994, Beier and Drennan 1997), but they also hunt in a variety of vegetative cover. For example, in eastern Oregon it was not uncommon to see goshawks hunting in open sagebrush (*Artemesia* spp.), and we often found ground-squirrels (*Spermophilus* spp.) in prey remains (Cutler et al. 1996). In addition, some of the most important prey of goshawks are lagomorphs and grouse, particularly snowshoe hares (*Lepus americanus*) and Ruffed Grouse (*Bonasa umbellus*). These species provide more biomass than most other prey, and reproductive output in goshawks may be negatively affected when large-biomass prey are not available (Doyle and Smith 1994, Iverson et al. 1996). Snowshoe hares and Ruffed Grouse inhabit early successional stage forest and are key species in the ten-year cycle in northern North America (Doyle and Smith 1994). There are also very important relationships between prey abundance and availability for foraging goshawks, and forest structure plays an important role in goshawk foraging habitat (Beier and Drennan 1997, DeStefano and Closkey 1997).

THE DATA WE NEED

Demography. Demographic data are vital, but studies must be properly designed and be long-term or the results are difficult, if not impossible, to interpret (DeStefano et al. 1994). A study of goshawk demography and habitat use on the Kaibab Plateau, which is probably the longest running study on the species to date, is approaching a long-term basis. However, funding waxes and wanes as the threat of listing the goshawk comes and goes (R.T. Reynolds pers. comm.). Unreliable funding for needed long-term studies is short-sighted and counter-productive. The U.S. Forest Service and other federal agencies must commit to studies that run greater than 10 years, as the answers we need cannot be determined in two to three years. Estimating the rate of population change (λ) for a species such as the goshawk may simply be too difficult and take too long for the listing process. Nonethe-

less, data on reproductive rates and survival are critical to understanding the ecology of goshawks and their likely response at a population level to changes in their habitat. It is worth considering if and how one can design and implement good demographic studies on goshawks before we dismiss them altogether.

Related to this, listing decisions based on migratory counts of goshawks would also be problematic, given the importance and influence of cyclic prey in the boreal forest and the capability of goshawks for long-range movements in response to declining prey. It would be difficult to assess trends in goshawk numbers based on migratory count data alone, even over a long period of time. However, migratory counts combined with other demographic data could provide important additional information on goshawks (Bildstein 1998).

Habitat. With some exceptions (e.g., *A. g. laingi* in southeast Alaska, *A. g. apache* in the Southwest), another study on nesting habitat of goshawks in the West may not be necessary. However, there remains plenty to learn regarding how juvenile goshawks use habitat within PFAs and how adults use habitat to forage. Also, very few habitat studies have been conducted in winter.

Documenting the distribution of all forest structural stages, including mature or old-growth forest, across the West would be an important step in the status review process. Such documentation will be important for a number of wildlife species, including goshawks, and has been suggested by Crocker-Bedford (1998) and Smallwood (1998). Recent efforts of the U.S. Fish and Wildlife Service in the latest review of the status of goshawks in the West showed how poorly information on forest stand structure is documented and/or available in a usable format (U.S. Fish and Wildlife Service 1998a). Low response rates on questionnaires sent to land management agencies and a wide variety of documentation, both in quality of information and methods used, make decisions on goshawk status based on habitat availability problematic. Although methods to gather and compile data on current forest conditions across the West need to be improved, future decisions on the status of goshawks ought not to be made based on the availability of old-growth forest alone. Concurrent data on demography and distribution of goshawks are also needed.

Prey. Because prey resources are so important to the population dynamics and distribution of goshawks, additional information on prey use, and the influence and interaction of prey abundance, availability, and habitat structure on goshawk populations, is needed. A multi-species approach, which includes predators, prey, and competitors, also moves us away from single-species management and more toward community and ecosystem approaches (Squires et al. 1998).

DISCUSSION AND CONCLUSIONS

There is little doubt that we have destroyed, fragmented, and otherwise altered old-growth forest in North

America (Norse 1990). In frustration to conserve remnant patches of old-growth, or any native ecosystem, the strongest tools of persuasion are going to be the ones most used. One such tool is the ESA. In the case of the Northern Spotted Owl and the temperate old-growth rainforest of the Pacific Northwest, this approach was prudent and necessary; listing the owl was the right course of action. However, before we take this action for the goshawk and list it as Threatened or Endangered, we need to ask if it is in the best interest of the species and the ESA itself. Listing decisions should be made regardless of politics (Sidle 1998), but politics are surely a part of the process, and political opposition to the ESA is real and strong. I am *not* advocating a weak stance on protecting species, just a reasoned one that considers our credibility as scientists and a judicious use of the ESA.

So, am I concerned about the status of goshawks in North America? Yes. Am I concerned about the loss of old-growth forest? Definitely. Should we list the goshawk to protect it and old-growth forest habitat? Probably not. This position may sound contradictory, given the case made for goshawks' use of old-growth forest, but it hinges on several considerations, such as the variety of structural stages that goshawks use, the importance of some early successional stage forest prey, the overwhelming pressure to list many species in the U.S.—several of which are truly threatened with extinction—that taxes our limited resources, and a concern that we invoke the ESA judiciously.

I recommend a different approach. I think there is time and opportunity to manage for goshawks in the West without listing. However, goshawks may currently be in the same position that spotted owls were in one to two decades ago. That is, some options remain, but if action is not taken now, far fewer options will be available later. To exercise some of our options now, I suggest the following: (1) provide funding and support to maintain current research similar to that on the Kaibab Plateau, and perhaps two or three additional and coordinated studies in other regions; (2) continue coordinated efforts to identify and map areas of remaining older forests across the West; (3) support the testing and evaluation of empirical habitat models that have been developed in the Southwest (Reynolds et al. 1992) and Northwest (McGrath 1997); (4) conduct on-site experiments to measure goshawk responses to silvicultural treatments; and (5) defer listing the goshawk under the ESA in favor of a coordinated national effort to assess habitat conditions, monitor populations, and evaluate habitat models and silvicultural treatment experiments (see Marzluff and Sal labanks 1998, Squires et al. 1998). Federal and state land management agencies as well as the timber industry should be involved in this process. We should keep in mind, however, that listing remains an option and perhaps a necessity, but one that should be based more on coordinated scientific efforts than political agendas from either side of the issue. Resource agencies need to make

firm commitments now to avoid listing the goshawk later. It would also be beneficial to avoid court, where "truth" is not always based on the best science, but rather the most forceful argument.

There is growing dissatisfaction with single species approaches to conservation and management. We need to pursue research and management at all levels of organization: populations, communities, and ecosystems. The goshawk is a good candidate for this multilevel approach. However, if we were to base our plans for the conservation and management of old-growth forest solely on the goshawk, we may not like what we get. It is true that mature forest is important around nest sites and as a component of foraging habitat, but ideal goshawk habitat may include a sizeable portion of the landscape in early seral stage forest to encourage high populations of important prey such as lagomorphs and Ruffed Grouse. The distribution of seral stages that may be good for goshawks, however, may actually include less old-growth than some other species require (possibly Pileated Woodpeckers [*Dryocopus pileatus*] and American marten [*Martes americana*]).

Implementing the above recommendations would take our collective will and effort, and it would mean that the land management agencies most involved with goshawks would need to be proactive and support research, adaptive management, and monitoring for more than a few years. Terms like "proactive" and "adaptive management" are often used, but these concepts would need to be translated into action on the ground (Marzluff and Sallabanks 1998). Such actions, of course, will take quite a bit of money, but I couldn't agree with Smallwood (1998) more when he states that adequate funding should be made available to ensure the viability of wildlife populations.

ACKNOWLEDGMENTS

I thank D.C. Crocker-Bedford, T. Bosakowski, M.H. Henning, P.L. Kennedy, J.M. Marzluff, and K.S. Smallwood for their thoughtful and constructive reviews. My special thanks to D.E. Varland for providing me the opportunity to air my views. Research on goshawks in Oregon was funded by the Nongame Program of the Oregon Department of Fish and Wildlife, U.S. Forest Service, U.S. Fish and Wildlife Service, Boise-Cascade Corporation, National Council for Air and Stream Improvement, and Center for Analysis of Environmental Change at Oregon State University. I appreciate the logistic support of the Oregon and Arizona Cooperative Research Units. This paper is dedicated to S.K. Daw, S.M. Desimone, and M.T. McGrath, the diligent graduate students who did all the work.

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BOOK REVIEWS

EDITED BY JEFFREY S. MARKS

J Raptor Res. 32(4):349
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The Raptors of Arizona. Edited by Richard L. Glinski. 1998. University of Arizona Press, Tucson, AZ. xv + 220 pp., 42 color plates by Richard Sloan, 42 range maps, 1 table, 1 appendix. ISBN 0-8165-1322-8. Cloth, \$75.00.—This is a handsome, well-written, and beautifully illustrated volume on the raptors of Arizona by people who obviously had their heart and soul in it. In terms of format, the book is a blend between popular and scientific literature. Twenty-seven contributors present the known information on each of 42 species of birds of prey. Each member of the 26 falconiforms, 13 strigiforms, and raptor-like 3 ciconiiforms are given two to five pages including description, distribution, habitat, life history, and status in Arizona. The authors often add their own personal observations and interesting notes on the ecology of each species.

According to the editor, Arizona is matched only by Texas in terms of raptor species diversity. This book is a superb compilation of that group. The 42 color plates by Richard Sloan are exquisite and in my mind reminiscent of the beautiful early paintings of Allan Brooks. The birds are presented in natural habitat settings in a characteristic behavior or attitude. Each painting nicely captures the essence of the species as viewed in Arizona habitats.

The introductory chapter provides a complete, yet succinct summary of what is to be expected. Included is a helpful map of the major Arizona river systems, mountain ranges, and important cities. The next chapter, entitled "Conservation of Arizona Raptors," provides the reader with an historic perspective about habitat change, raptor population changes, and how little we really know about even the recent past. The editor provides an excellent overview of the various ways that mankind has negatively affected (habitat loss, contaminants, electrocution, shooting) raptor populations, but in my opinion he could have developed

a more positive assessment for at least some of their futures. For instance, the use by many raptor species of man-made nest structures and use of urban environments could have been highlighted in this chapter. Table 1, the only table in the book, provides handy information on habitat and seasonal occurrence.

The next chapter, "Habitats of Arizona Raptors" by D.E. Brown, provides concise and informative descriptions of 19 habitats. These descriptions undoubtedly will be helpful to people not familiar with the diversity of Arizona's habitats and topography. Each habitat receives a description of vegetation, elevation, and weather conditions. The end of this chapter includes a discussion of factors influencing raptor distribution.

An informative chapter on the details of where to find raptors is presented by S.W. Hoffman. Included are all the known raptor hot spots whether they be breeding areas, migratory flyways, or wintering areas. J.W. Dawson and B.D. Taubert provide a good overview of contemporary falconry in Arizona in the following chapter, and A.M. Rea provides a short introduction to the New World Vultures.

A central goal of this book is to "enhance public awareness of these species, enticing readers to go out and discover these birds in the wild and help ensure their presence in Arizona skies." To this end the editor, artist, and authors have easily succeeded. A pleasure to read and to look at, this book will fill out your "raptors of the southwestern United States" interests. Apparently very much a collaborative effort by the editor, authors, Arizona Wildlife Foundation, Arizona Game and Fish Department, and University of Arizona Press, this book could serve as the standard for what I would hope will be future efforts in other states to promote the appreciation of raptors. For those of you interested in natural history, ornithology, and birds of prey, this book is a must for your library.—Peter H. Bloom, Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, CA 93010 U.S.A.

J. Raptor Res. 32(4):350
© 1998 The Raptor Research Foundation, Inc.

The Long-eared Owl. By Derick Scott. 1997. The Hawk and Owl Trust, London. xv + 128 pp., 29 color photographs, 2 range maps, 2 appendices, numerous black-and-white illustrations. ISBN 0-9503187-7-9. Cloth, £17.95 (U.K.).—Derick Scott has studied Long-eared Owls (*Asio otus*) in Britain for 45 years and perhaps has spent more time observing this species than anyone else on earth. His work is mentioned in Stanley Cramp's *The Birds of the Western Palearctic* and in David Glue's papers on Long-eared Owls, but little of Scott's research has appeared in the refereed literature. Here, Scott distills his observations into the first book devoted to this interesting and somewhat enigmatic species.

Focusing on Long-eared Owls in Britain, 10 chapters present general information on appearance, population status, distribution, food habits, habitat and home range, breeding biology, behavior, vocalizations, mortality and conservation. The book concludes with an appendix that catalogues diseases and parasites that have been documented in Long-eared Owls and another that lists scientific names of species mentioned in the text. The color photographs by Scott are excellent, as are Dan Powell's black-and-white illustrations.

Because the book is written for the layperson, almost no hard data are presented. Instead, the book consists of a free-flowing narrative, some of which is based on published work or personal communications from others, and some taken from Scott's own experiences. A "Selected Bibliography" lists 36 books and 98 journal references, most of which are not cited in the text. Moreover, no fewer than 19 of the articles that *are* cited in the text *are not* included in the list of references! This informal style makes for easy reading, but the lack of detail regarding methods of study and docu-

mentation of results leaves many questions unanswered. Most important, nowhere is it mentioned that Scott has ever banded a Long-eared Owl. At the very least, it would seem that most of his observations were of unbanded individuals. Scott states that males sometimes incubate eggs and brood young, behaviors that have not been documented in studies of marked owls. Similarly, he believes that mate and site fidelity are the rule in British Long-eared Owls, which is quite the opposite from the situation in North America and Europe. He also states that incubation typically does not begin until the clutch is complete. Again, this has never been seen elsewhere. Finally, Scott presents some largely unconvincing evidence that Long-eared Owls sometimes move eggs and young among nests (similar reports have been published for nightjars and later found to be untrue). Are Long-eared Owls in Britain really that different from those elsewhere? Perhaps so, but one wonders why so many of these seemingly fantastic observations have not appeared in the refereed literature. The main problem is that these behaviors can only be documented with marked individuals (aside from the issue of when incubation begins); without such evidence, the behaviors in question must be considered hypothetical.

Because of these potential problems, I am at a loss to identify a readership who will benefit from this book. The text will be of interest to nonprofessionals, who unfortunately are likely to accept at face value the undocumented statements therein. The lack of documentation of the results makes the book unsuitable for professionals. Having said this, I must admit that I enjoyed the book because I identified with many of the experiences that Scott describes. Clearly, he is a keen observer with a strong dedication to conservation. Read the book if you must, but do not hesitate to question some of its conclusions.—Jeff Marks, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812 U.S.A.

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The *Journal of Raptor Research* (JRR) publishes original research reports and review articles about the biology of diurnal and nocturnal birds of prey. All submissions must be in English, but contributions from anywhere in the world are welcome. Manuscripts are considered with the understanding that they have not been published, submitted or accepted for publication elsewhere. Manuscripts are subjected to peer review for evaluation of their significance and soundness, and edited to improve communication between authors and readers. Decisions of the editor are final.

Material is published as feature articles, short communications (usually not longer than two printed pages), and letters (see recent issue of the JRR for examples).

Submissions that adhere closely to the JRR's format greatly enhance the efficiency and cost of the editorial and publishing processes. Author's efforts in this regard are deeply appreciated by the editorial staff.

When submitting scholarly papers, send the original and three copies, a completed checklist (see below), and a cover letter that includes: (1) a statement that the data in the manuscript have not been published or accepted for publication in the same form, and have not been submitted simultaneously elsewhere, (2) the name and address of the corresponding author (in multiauthored papers) including any temporary addresses where that author will be during the review process (also the phone number and, if possible, a FAX number and e-mail address of the corresponding author), and (3) if applicable, any special instructions. Authors may also suggest potential reviewers.

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JOURNAL OF RAPTOR RESEARCH**CHECKLIST FOR PREPARATION OF MANUSCRIPTS***(check items and submit with manuscript)***I. GENERAL INSTRUCTIONS**

(Consult recent issues for additional guidance on format)

- Type manuscripts on one side of either 216 × 278 mm (8.5 × 11") or standard international size (210 × 297 mm) good quality paper (do not use erasable or lightweight paper). Word-processor-generated manuscripts must be done with a letter-quality or near-letter-quality printer. DOUBLE SPACE THROUGHOUT including title, text, tables, figure legends, and literature cited.
- Give the scientific name at the first mention of a species, both in the abstract and in the article. Scientific names of birds should follow the usage of the *AOU Check-list of North American Birds* (7th. ed. 1998 and subsequent supplements in the *Auk*) or an authoritative source corresponding to other geographic regions. Do not give subspecific identification unless it is pertinent. Use lower case for all common names, including birds.
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- Use "Figure" only to start a sentence; otherwise "Fig." if singular, "Figs." if plural (e.g., Fig. 1; Figs. 2,3; Figs. 4–6).
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- Use these abbreviations without spelling out: hr, min, sec, yr, mo, wk, d, km, cm, mm; designate temperature as 32° C.
- Use "continental" dating (e.g., 10 July 1993, 1–3 June, 11 May to 11 June).
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- Assemble manuscripts for regular articles in this order: (1) title page, (2) abstract page, (3) text, (4) tables, (5) figure legends, (6) figures. DO NOT STAPLE.

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- For regular articles, include an abstract of about 250 words in one paragraph that is completely without reference to the text. Be concise, include the paper's purpose, but emphasize the results. Statements like "results will be discussed" are not appropriate. The abstract will also be published in Spanish. Authors fluent in both languages are encouraged to include both versions, otherwise the JRR will provide the Spanish translation.
- Include five to seven key words for indexing after the abstract.
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Avoid citing references in the abstract. If they must be cited, include journal name, volume, pages, and year, all in parentheses.

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BY ELISE VERNON SCHMIDT

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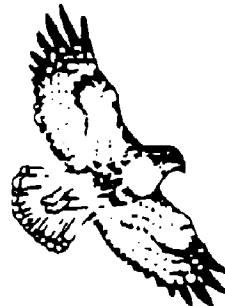
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